Ichthyoliths and Other Microvertebrate Remains from The Morrison Formation (Upper Jurassic) of Northeastern Wyoming: A Screen-Washed Sample Indicates A Significant Aquatic Component to the Fauna

By: **Andrew B. Heckert** & John R. Foster

Abstract

A screenwashed microvertebrate site, the Mile 175 locality, in the Morrison Formation of Wyoming has yielded more than 3000 elements of actinopterygian fish and indicates that fish were not as rare in some parts of the formation as previously supposed. Actinopterygians are represented by diverse teeth and tooth-bearing bone fragments, fin elements, and thousands of scales and scale fragments that can be divided into three distinct morphotypes. Lungfish are rare, represented by nine toothplates and toothplate fragments that are provisionally assigned to Potamoceratodus. Tetrapods recovered from the Mile 175 locality include indeterminate salamanders, turtles, choristoderes, a squamate, goniopholid crocodyliforms, theropod and ornithopod dinosaurs, and several mammals, including Docodon and indeterminate multituberculates. Salamanders are represented by just a few indeterminate vertebrae. The turtle fauna includes numerous small shell fragments and limb elements. The authors assign a tooth-bearing jaw fragment and several vertebrae to the choristodere Cteniogenys, whereas a sole vertebra is the only squamate fossil recovered. Theropod dinosaurs are well represented by several teeth, as is the ornithopod dinosaur Othnielosaurus. Similarly, several mammalian tooth and jaw fragments can be referred to either Docodon or Multituberculata indet. Dominance of the sample by aquatic and semi-aquatic taxa suggests the paleodepositional environment was a permanent water source. Many of the specimens appear to represent small and presumably ontogenetically young individuals of larger, known taxa in the Morrison Formation, and the site includes the northernmost occurrences of several taxa in the formation. Screenwashing efforts at several other previously quarried large-vertebrate sites in the Morrison Formation have shown promising results for recovering previously unidentified taxa.

Andrew B. Heckert & John R. Foster (2011) "Ichthyoliths and Other Microvertebrate Remains from The Morrison Formation (Upper Jurassic) of Northeastern Wyoming: A Screen-Washed Sample Indicates A Significant Aquatic Component to the Fauna" *Palaeogeography, Palaeoclimatology, Palaeoecology* Volume 305 pp. 264-279 [doi:10.1016/j.palaeo.2011.03.007] Version of Record Available From (www.sciencedirect.com)

1. Introduction

The Upper Jurassic Morrison Formation (Kimmeridgian–Tithonian) is well known for its dinosaur fauna consisting of a diversity of large sauropods, many theropods, ornithopods, ankylosaurs, and stegosaurs (Dodson et al., 1980; Russell, 1989; Carpenter et al., 1998; Chure et al., 2006). A number of individual sites have filled in our knowledge of the contemporary small vertebrate and non-dinosaurian aspects of the paleofauna of the Morrison Formation, and these indicate the presence of ray-finned fish, lungfish, salamanders, frogs, turtles, crocodylians, choristoderes, and more than 20 species of mammals (Foster, 2003; Chure et al., 2006). These small vertebrates historically have been less abundant in the rocks of the Morrison Formation overall, but this is in part due to collecting bias (Foster, 2003; Foster and Trujillo, 2004); some sites contain large samples of small- and microvertebrates. For example, Quarry 9 at Como Bluff has yielded more than 3000 vertebrate specimens, mostly small (Carrano and Velez-Juarbe, 2006), and by far most were collected by hand quarrying. Screenwashing of sites in the Morrison Formation thus has been carried out sporadically and often unsuccessfully, but as is documented here, such operations can yield large samples of small vertebrates.

Dodson et al. (1980) noted the paucity of crocodiles, turtles, and fish in the Morrison Formation, as compared to their relative abundance in other Mesozoic formations in North America, such as the Upper Cretaceous Hell Creek Formation. These taxa may be part of the low-density background of small-vertebrate remains that Dodson et al. (1980) noted was rare in the Morrison Formation in their Lithofacies C (drab mudstone). Work in the last 25 years has demonstrated that the small vertebrates and aquatic taxa may not be as rare as they appeared at that time. Many small, isolated fish occurrences in the Morrison Formation have never been reported in the literature, but articulated occurrences of fish are indeed extremely rare. A hard, calcareous siltstone layer just above the Mygatt–Moore

Quarry in the Brushy Basin Member of the Morrison Formation in Rabbit Valley, western Colorado (Foster et al., 2007), has produced articulated skeletons of paleoniscoids and teleosts (*Morrolepis schaefferi*, *Hulettia hawesi*, cf. *Leptolepis*) (Kirkland, 1998). The Temple Canyon site in central Colorado has produced a different paleofauna of many articulated fish and at least one lungfish skull from the lower part of the formation (Gorman et al., 2007). Other sites have abundant, but fragmentary fish remains that are difficult to identify to lower taxonomic levels. For example, several hundred amioid vertebrae are known from the collections of Quarry 9 at Como Bluff in Wyoming, although this is rarely reported (Kirkland, 1998; Foster, 2003; Carrano and Velez-Juarbe, 2006). The Ninemile Hill site in Wyoming preserves many fragmentary fish remains as well (Trujillo, 1999). Many fish remains are delicate and microscopic and may well be recognizable only through picking of screen-washed matrix.

Here we report on a microvertebrate fauna of some 4300+ specimens from the Morrison Formation at the Mile 175 locality in the Black Hills of northeastern Wyoming (Fig. 1). The specimens were collected largely by screen-washing weathered mudstone in the Morrison Formation. The fauna contains a predominance of fish and other aquatic vertebrates rarely seen in most Morrison Formation quarries. A similar abundance, taxonomic composition, and mode of preservation is present at the Ninemile Hill locality in Wyoming (Trujillo, 1999), and we suggest that such occurrences may not be rare if specifically sought out. We also note here that not only are microvertebrates from the Morrison Formation seldom reported in the literature, but even fewer are illustrated. Here we use scanning electron microscopy (SEM) technology to collect images of representative faunal elements to facilitate further comparison in future studies. Throughout this paper the authors will refer to the many different Morrison Formation localities by their names as published by Foster (2003) and subsequent workers, recognizing that many of these localities have been worked by multiple parties from different institutions.

1.1. Institutional abbreviations

CMC, Cincinnati Museum Center; DNM, Dinosaur National Monument, Vernal; FMNH, Field Museum of Natural History, Chicago; LACM, Natural History Museum of Los Angeles County; MWC, Museum of Western Colorado, Fruita; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque; SDSM, South Dakota School of Mines and Technology Museum of Geology, Rapid City; UCM, University of Colorado Museum, Boulder; UFHNH, Utah Field House of Natural History, Vernal; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; UW, University of Wyoming Department of Geology and Geophysics Collection of Fossil Vertebrates, Laramie.

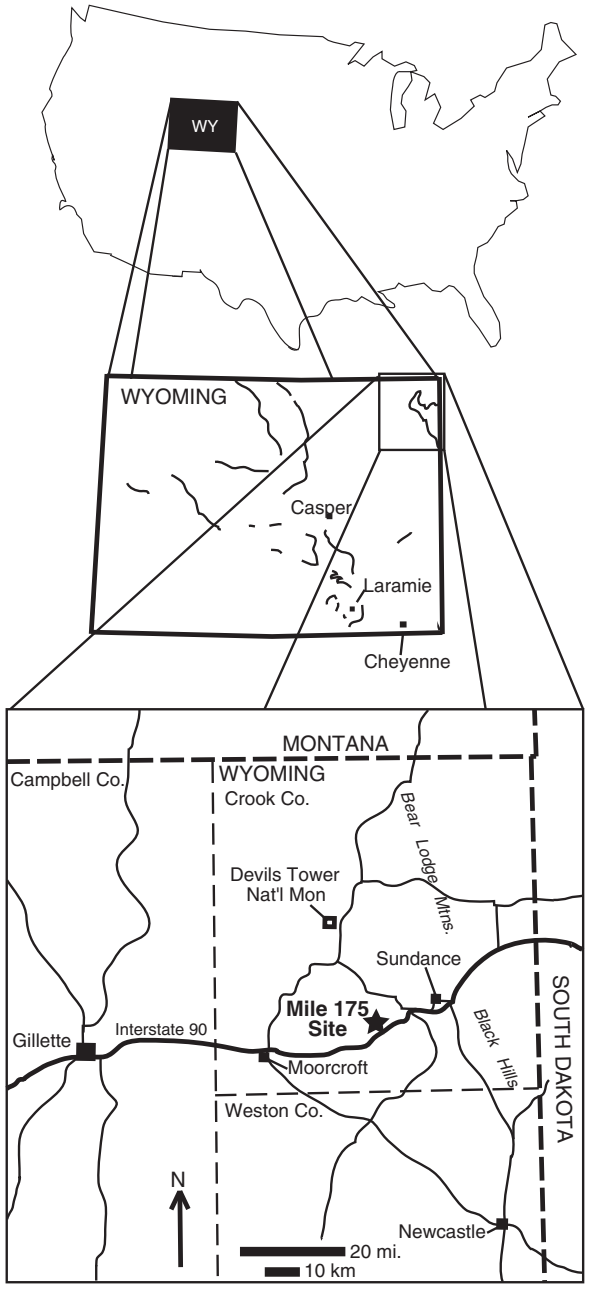

Fig. 1. Map showing location of the Mile 175 site (star) in northeastern Wyoming. State map shows cities, major Morrison Formation outcrops, and inset area.

2. Previous studies

Screen-washing of sediments from the Morrison Formation has been carried out by various groups on some occasions and sometimes on a fairly significant scale with wildly disparate results (Table 1). In comparison with operations in nonmarine Upper Cretaceous formations of the American West, however, work in the Morrison Formation has been limited. In the 1960s, Bill Turnbull of the Field Museum of Natural History screenwashed the spoil piles of Como Bluff's Quarry 9 with some success, producing a collection of several mammal jaws and teeth and other small vertebrate elements. At the Fruita Paleontological Area, George Callison's crews screenwashed matrix during parts of two seasons but found that little of the material survived the soaking intact, and they soon returned to hand quarrying (G. Callison, pers. comm., 2009). Kelli Trujillo and one of us (JF) did a test wash of a very limited amount of matrix (part of one Ziploc bag) from the Callison (Main) Quarry at the Fruita Paleontological Area several years ago and found several fish scales. In the 1970s, Ken Carpenter (then at the University of Colorado) screenwashed ~20 kg of matrix from a locality in the Freezeout Hills of Wyoming and found at least one mammal tooth. By the early 1990s a significant screenwashing program was in place for the Rainbow Park microvertebrate sites (particularly RP 94) at Dinosaur National Monument. Although screenwashing produced many specimens there, the best material was found by hand quarrying RP 96. In the late 1990s, Kelli Trujillo screenwashed Ninemile Hill in Wyoming (Trujillo, 1999) and produced a microvertebrate fauna similar to what is reported here from Mile 175. Screenwashing by the Museum of Western Colorado of two five-gallon buckets of matrix from the Cleveland–Lloyd Quarry in Utah recently produced roughly 200 dinosaur and other bone fragments, about half of them very small, including one crocodilian osteoderm, one shell fragment of a juvenile turtle, and one half-vertebra of a very small reptilian, possibly *Cteniogenys*. Limited test

Table 1
Summary of screenwashing studies in the Morrison Formation (with one dry-screening site included). Institutional abbreviations: see text. Vertebrate group abbreviations in Results: A, amphibians; C, choristoderes; E, eggshell; F, fish; L, lizards; M, mammals; R, reptiles, indet. small; S, sphenodontians. * = dry screened.

Locality	Workers/institution	Results	Key references
Ninemile Hill	Trujillo, UW	Abundant microverts: F, A, S, L, C, M, R	Trujillo (1999)
Rainbow Park	Madsen, Elder, Chure, DNM	Abundant microverts: F, A, S, L, M	Chure and Engelmann (1989)
Mile 175	Foster, SDSM, UW, MWC	Abundant microverts: F, A, L, C, E, M, R	This paper
Little Houston Quarry	Foster, MWC	Abundant microverts: F, A, S, L, C, M, R	Foster (2001)
Fruita Paleo Area	Callison, LACM	Limited microverts: F	See text
McKinsey–REX	Trujillo, UW	Limited microverts: F	See text
Freezeout Hills	Carpenter, UCM	Limited microverts: M	See text
Cleveland–Lloyd	Foster, MWC	Limited microverts: C?	See text
Mygatt–Moore	Foster, MWC	Limited microverts: E, R	See text
Reed's Quarry 9	Turnbull, FMNH	Moderate microverts: M, R	See text
Fox Mesa*	Brett–Surman, USNM	Moderate microverts: S, E, M	Brett-Surman et al. (2005)
North of DNM	Sroka, UFHNM	Pending	See text
Aaron Scott Site	Esker, CMC	No identifiable material	Esker (2009)
Peterson Quarry, NM	Heckert, NMMNH	None	None

screening of matrix from the Mygatt–Moore Quarry produced one piece of eggshell and a small (2 mm) and as yet unidentified reptilian tooth. The Fox Mesa site in northern Wyoming has produced many mostly terrestrial microvertebrates through hand quarrying and dry-screening (Brett-Surman et al., 2005). Personnel at the UFHNH have recently begun screenwashing a site in the Morrison Formation near Dinosaur National Monument, but results are still preliminary. Screenwashing of jacket matrix of the McKinsey-REX Dinosaur Quarry near Laramie, Wyoming, produced several actinopterygian fish teeth but was discontinued due to otherwise barren results (Trujillo, pers. comm., 2011). Screenwashing of the Aaron Scott Site in the San Rafael Swell area of Utah (Esker, 2009) has not yet produced identifiable material. A very small (<2 kg) sample from the Peterson Quarry in New Mexico did not yield any fossils. The authors are not aware of any other screenwashing operations in the Morrison Formation.

In the cases of Quarry 9 and the Fruita Paleo Area, more material was found at the site through hand quarrying than through the screenwashing operations. At Rainbow Park, the quality if not the amount of material hand quarried from RP 96 exceeded that produced by screenwashing. Only the collection from Ninemile Hill was obtained almost exclusively through screenwashing, and other than Trujillo's (1999) master's thesis and several publications on the Rainbow Park sites (Chure and Engelmann, 1989; Chure et al., 1989; Chure, 1994), few of the results of this screenwashing work have been published.

3. Setting

The Mile 175 locality is in southern Crook County, Wyoming, approximately 18 miles east of Moorcroft (Fig. 1) on the western flank of the Black Hills. The Morrison Formation in this part of the Black Hills is underlain by the Sundance Formation and is overlain by the Lakota Formation. The producing layer is in a soft, light greenish-gray mudstone apparently in the upper levels of the Morrison Formation, but its exact stratigraphic position has not been determined due to cover above and below the outcrop. In any case, correlation with other Morrison Formation outcrops to the south and west is complicated by the fact that the formation is relatively thin (only 21–39 m thick) in the Black Hills region (Mapel and Gott, 1959; Mapel and Pillmore, 1963), probably due to post-depositional erosion (F. Peterson, pers. comm., 1997). The site is several miles east of, and apparently stratigraphically above, the rich and taxonomically diverse sample at the Little Houston Quarry (Foster and Martin, 1994; Foster, 2001).

Steve Sroka and Russ Jacobson discovered the Mile 175 site in 1993, and one of us (JF) has collected there most years with several institutions in connection with on-going paleontological study of the Morrison Formation of the Black Hills. A number of vertebrate taxa have been identified from the site, along with fragments of bivalve shells. The fossils are part of a Type III deposit (Foster et al., 2006a) consisting of soft mudstones that screenwash easily. Such deposits are different from the dense accumulations of disarticulated bones of microvertebrates seen at sites like Quarry 9, the Small Quarry, and the Little Houston Quarry and from the much less dense accumulations of sometimes articulated bones and whole skeletons such as those that occur at sites like the Fruita Paleontological Area, Wolf Creek, and Rainbow Park (Foster et al., 2006a; Kirkland, 2006). Material from the Mile 175 site is cataloged at MWC, SDSM, and UW.

4. Methods

The Mile 175 locality is often regenerated in surface fossil production by seasonal precipitation; it has been collected most years since the study began, usually starting with surface picking of newly exposed material, which typically consists of turtle shell fragments and small reptile vertebrae. After surface material was cleared, 5 gal buckets were filled with soft (weathered) surface mudstone shoveled in from the producing layer (top 10–15 cm). The total amount of matrix processed so far consists of six 5-gallon buckets and one 50-pound (~20 kg) burlap sack; each was filled with surface (weathered) material, and workers have never needed to dig in deep into the outcrop. As such, the sampling method employed so far may be considered a qualitative surface collection (Peterson et al., 2009).

Screen-washing and sorting consisted of: 1) soaking the mudstone matrix in 1 × 1 mm mesh screen boxes in water for 1 h (longer and repeated cycles if needed); 2) gentle down-up agitation only (pushed down, lifted slowly clear of the surface, set floating in water, pushed down again), until fine clays were washed clear; 3) drying the concentrate outside in the sun; and 4) picking under a Meiji microscope at 7–45× magnification. Screens were loaded lightly (one scoop of matrix per box) and were not shaken laterally. This usually resulted in a decrease in matrix volume of approximately 66%.

The images of fossils presented here were shot by one of us (ABH) at Appalachian State University's College of Arts and Sciences microscopy facility using a Quanta 200 ESEM utilizing XT Microscope Server imaging software. All specimens were imaged without coating with the ESEM in low vacuum mode and operating at 15–20 kW. Images were captured as ~3.7 MB 8-bit .tif files, and all subsequent image manipulation and compilation was accomplished in Adobe Photoshop CS3 on a MacIntosh operating system.

Systematics is based on Patterson (1982), Schaeffer and Patterson (1984), Kirkland (1987, 1998), and Grande and Bemis (1998) for fish; Evans et al. (1988) for caudates; Hay (1908), Gaffney (1979), and Joyce (2007) for turtles; Evans (1994) for squamates; Steel (1973), Evans (1991), Chure and Evans (1998), Weishampel et al. (2004), and Galton (2007) for archosauromorphs, including crocodyliforms and dinosaurs;

and Simpson (1929) and Kielan-Jawarowska et al. (2004) for mammals. Identifications follow these and other references cited in the relevant text.

5. Results

Table 2 shows the vertebrate paleofauna known thus far from Mile 175. There are at least 14 taxa represented. Table 3 records the number of identified specimens of each group and shows the dominance of fish material from the sample. The record of each group will be discussed in the following section.

5.1. Osteichthyes, Actinopterygii

Both actinopterygian and sarcopterygian fish are known from the site, mostly in the form of ichthyoliths, which are defined as microscopic skeletal remains of fish, mainly dermal denticles, scales, and teeth (Tway, 1984; Tway et al., 1986). Actinopterygian fish specimens are by far the most abundantly preserved vertebrate elements at Mile 175. Preserved bones include jaw fragments, isolated teeth, fragments of flat bones with tooth patches, scales of three types, possible skull bone fragments, and fin ray elements. Vertebrae are surprisingly rare. Jaw fragments include seven dentary or maxilla pieces with one or several teeth still attached to the bone in an acrodont condition. There are more than 160 isolated teeth of indeterminate actinopterygians in the sample, similar to MWC 5948 (Fig. 2A–C) in each having a conical shape, with crown height ranging from less than 1 mm to several millimeters, and a tip consisting of clear, tapering acrodin, a material indicative of actinopterygians (Tway et al., 1986; Smith and Zatoń, 2007).

Flat bones containing tooth patches in actinopterygians such as amioids include the vomers, parasphenoids, pharyngeal plates, dermopalatines, ectopterygoids, endopterygoids, and metapterygoids in the skull and the coronoids and prearticulars in the lower jaw (Grande and Bemis, 1998). These are, of course, in addition to the lines of teeth in the marginal dentition. The tooth patch-bearing flat bone fragments in the sample from Mile 175 (Fig. 2D–I) are sometimes less than 1 mm across and contain teeth with blunt to pointed and tapered tips. MWC 5950 (Fig. 2D–F) is barely more than 1 mm in its longest dimension and contains nine teeth, whereas UW 18149 (Fig. 2G–I) is less than 1 mm across and contains six teeth of various diameters. These two specimens are just a representation of the dozen or so similar specimens in the sample, and although the fragmentary nature of the fossils renders identifying specific bones difficult, the relative abundance of these fossils in the screenwashed sample suggests many actinopterygian skull fragments were fossilized at the site.

Actinopterygian scales are by far the most abundant elements in the Mile 175 sample, accounting for literally thousands of fragmentary specimens. These scales are of three types and are similar to those identified in much smaller numbers by Kirkland (1998) from the Fruita Paleontological Area in Colorado. Most scales are broken, ~1–4 mm across, and are thin, flat elements with smooth internal surfaces and an external surface with characteristic texture. The first type of scale (e.g., MWC 5276; Fig. 3) is composed of wavy ridges and is similar to those of amioids (Schultze, 1996; Kirkland, 1998); the second type of scale (MWC 5277; Fig. 4) contains an ornament of short, blunt spines; and the third type consists of diamond-shaped scales with a very smooth, shiny external surface of ganoine. These three types, respectively, are also equivalent to the first through third types Kirkland (1998) described and illustrated. At the Mile 175 site the first and second types of scales are approximately equally abundant (~1700 specimens each) and the third type somewhat less so (~450 specimens), but the sample overall suggests that at least three types of actinopterygians were present at the site, including, probably, amioids. Some of the flat, ornamented pieces identified here as scales of the first and second types do bear general similarities to fragments of some actinopterygian skull elements, and we do not rule out the possibility that some skull bone fragments are included in the sample. Regardless of the elemental assignment, all belong to actinopterygians.

The presumed fin ray elements are generally small, mm-scale or less, rectangular to square bones with slightly constricted midsections, flattened ends, and convex to flat surfaces. Although it is not known with certainty what these 60+ elements are, they appear most similar to the small plates that, formed up in long lines, comprise the fin rays of actinopterygian fish of this age (Schaeffer and Patterson, 1984).

Known actinopterygians from the Morrison Formation include large amioids from Bone Cabin Quarry, Quarry 9, and other sites, a pycnodontid, and the genera *Morrolepis*, cf. *Hulettia*, and cf. *Leptolepis* from the Mygatt–Moore Quarry and Fruita Paleontological Area in western Colorado (Kirkland, 1998, 2006). Articulated actinopterygians are also known from the Temple Canyon site near Cañon City, Colorado (Small et al., 2007).

Table 2
Vertebrate faunal list for the Mile 175 locality.

- Osteichthyes
  - Actinopterygii
    - Amioid indet.
    - Indet. A (scale morphotype 1)
    - Indet. B (scale morphotype 2)
  - Dipnoi
    - *Potamoceratodus* sp.
- Amphibia
  - Caudata indet.
- Reptilia
  - Testudinata
    - *Glyptops* sp.
    - *Dinochelys* sp.
    - Testudinata indet.
  - Squamata indet.
  - Archosauromorpha
    - Choristodera
      - *Cteniogenys* sp.
  - Archosauria
    - Crocodyliformes
      - Neosuchia
        - Goniopholididae indet.
    - Crocodyliformes indet.
    - Dinosauria
      - Theropoda indet.
      - Ornithopoda
        - Hypsilophodontidae
          - *Othnielosaurus* sp.
    - Dinosauria indet.
      - Indet. eggshell
- Mammalia
  - Docodonta
    - *Docodon* sp.
  - Multituberculata indet.
  - Mammalia indet.

Table 3
Microvertebrate fossils recovered from the Mile 175 locality.

Taxon	No. of specimens	Percent of sample	Preserved elements
Actinopterygii	4198	96.5%	Scales, teeth, jaw fragments, fin elements, and tooth patch fragments
Potamoceratodus	9	0.2%	Tooth plates
Testudinata	31	0.7%	Shell fragments, limb elements
Cteniogenys	8	0.2%	Vertebrae, jaw fragment
Crocodyliformes	67	1.5%	Teeth, osteoderms
Theropoda	8	0.2%	Teeth
Othnielosaurus	10	0.2%	Teeth
Mammalia	14	0.3%	Teeth, jaw fragments, caudals
Caudata	6	0.1%	Vertebrae
Squamata	1	0.02%	Vertebra

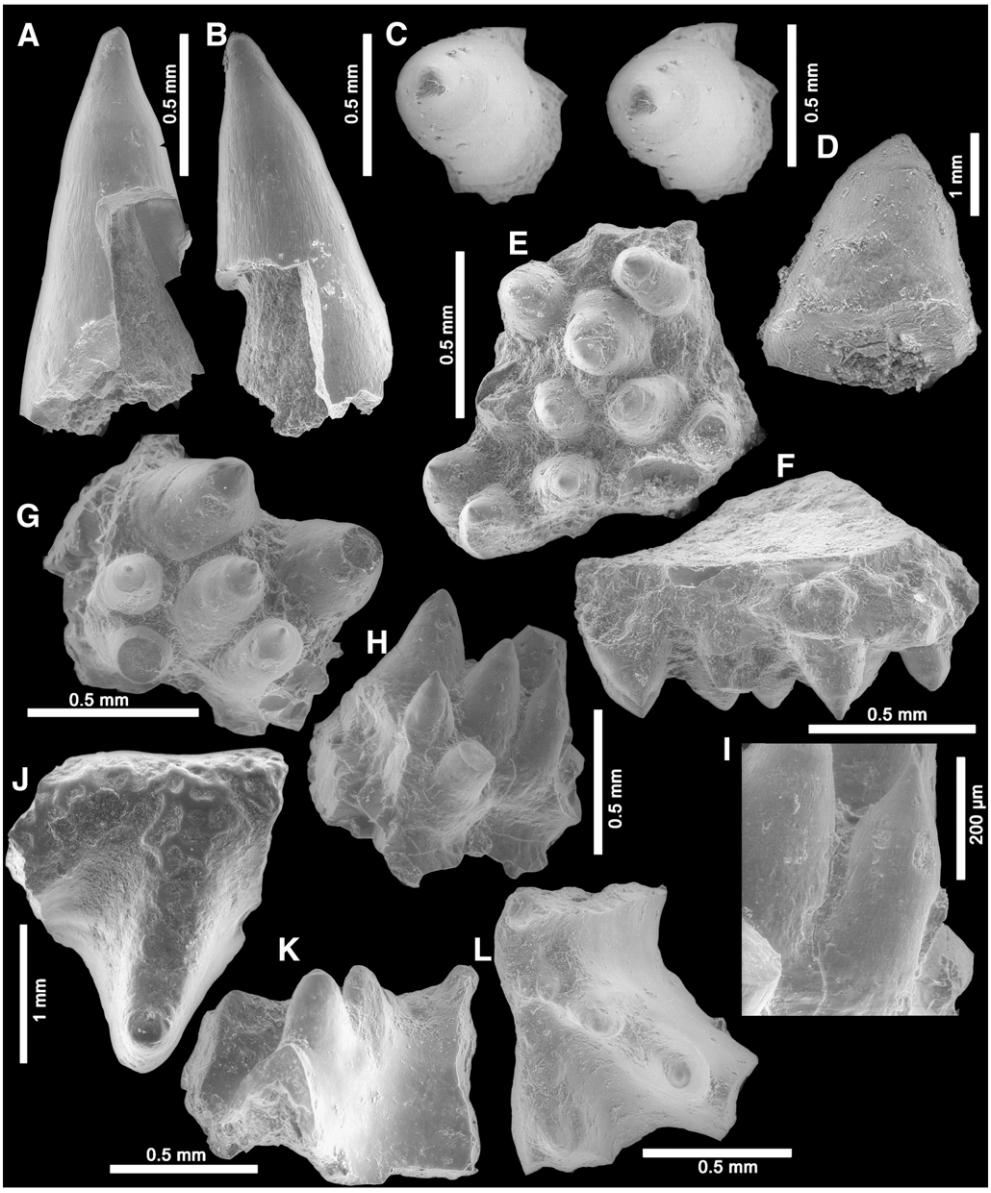

Fig. 2. Osteichthyans from the Morrison Formation, Mile 175 locality, Crook Co., Wyoming. A–C, Actinopterygian tooth (MWC 5948) in A, labial, B, lingual, C, stereo occlusal views; D–F, Actinopterygian tooth patch fragment (MWC 5950) in D, isolated tooth in side view, E–F, palatal fragment in E, occlusal, and F, side views; G–I, Actinopterygian tooth patch fragment (UW 18149) in G, occlusal, H, oblique side, and I, close-up views; J, *Potamoceratodus* dental plate (UW 18261) in occlusal view; K–L, possible *Potamoceratodus* dental plate fragment (MWC 5853) with enameloid in K, side, and L, occlusal views.

5.2. Osteichthyes, Dipnoi

Lungfish are also represented in the sample from Mile 175 by tooth plate fragments assigned to *Potamoceratodus* sp. Among the nine specimens known so far, larger individuals are represented by tooth plate fragments up to a couple millimeters across (still small) containing the ridges and dimpled enamel typical of such lungfish elements (UW 18261; Fig. 2J). Juvenile lungfish are represented by small (<1 mm fragments such as MWC 5853), thin tooth plates with smoother surfaces than in adults and with tubercles (tooth-like bumps) along the ridges (Fig. 2K–L). The lungfish fauna from the Morrison Formation includes several species originally assigned to *Ceratodus* (Marsh, 1878; Kirkland, 1987, 1998), including the very large *C. robustus*. "*Ceratodus*" *guentheri* was recently assigned to the new genus *Potamoceratodus* (Pardo et al., 2010), which probably includes most species of lungfish from the Morrison Formation except, possibly, *Ceratodus robustus*. The tooth plates from Mile 175 are similar to *Potamoceratodus* and distinct from *C. robustus*; they appear to be significantly smaller than the average for the formation and may represent a high percentage of juveniles and other young individuals.

5.3. Osteichthyes indet., Dipnoi?

One indeterminate, possibly osteichthyan element in the sample is MWC 5854, a long, laterally compressed apparent tooth element with four conical, linearly arranged cusps (Fig. 5A–B). It is asymmetrical, with one vertical and one less steeply dipping side (Fig. 5C–D). It is unknown for certain whether this is an actinopterygian tooth element, a dipnoan tooth, or something else, but the longest dimension of the fossil is only ~2 mm. It does not appear to pertain to a tetrapod. Comparison with marginal and pterygoid tooth plates of dipnoans from the Permian of Kansas (Hembree et al., 2005) indicates some similarities, and it is similar in some ways to juvenile dipnoan vomerine teeth.

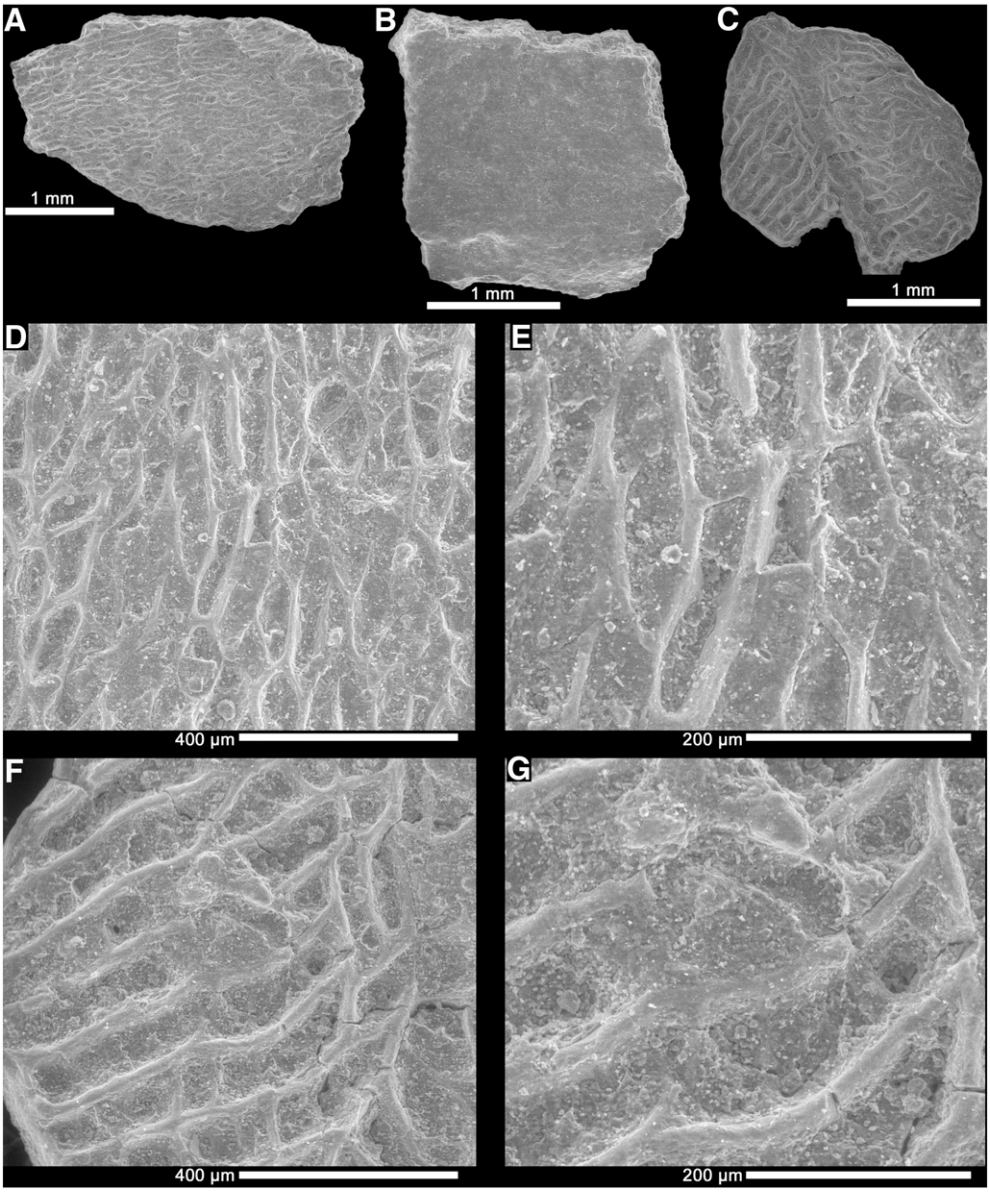

Fig. 3. Osteichthyan scales from the Morrison Formation, Mile 175 locality. A, MWC 5276A (external view); B, MWC 5276B (internal view), C, MWC 5276C (external view). D–E, close-ups of MWC 5276A in higher magnification views; F–G, MWC 5276C in higher magnification views. These are similar to "first type" of Kirkland (1998) from the Fruita Paleontological Area.

5.4. Amphibia, Caudata

So far, no frogs have been recovered from the Mile 175 fauna, but salamanders (Caudata) are represented by six small, unassociated vertebrae with deeply amphicoelous centra and stout, dorsoventrally elongate transverse processes. These vertebrae are generally similar to those of modern salamanders and others from the Late Jurassic. The Morrison Formation contains several known genera of caudates, but only one currently valid taxon, *Iridotriton*, has been named (Evans et al., 2005).

5.5. Reptilia, Testudinata

Turtle specimens (31 total) include some limb elements but are mostly shell fragments. Several shell fragments have been identified as *Glyptops* and others as *Dinochelys* on the basis of shell ornamentation (Gaffney, 1979), but the majority of shell specimens (and all limb elements) are identified as Testudinata indeterminate. In addition to *Glyptops* and *Dinochelys*, the Morrison Formation has yielded the rare turtles *Uluops* and *Dorsetochelys* (Bakker et al., 1990; Foster, 2003).

5.6. Reptilia, Squamata

A single specimen assigned to Squamata indeterminate consists of a small vertebral centrum that is distinctly procoelous. Although this specimen cannot be more specifically identified, there are at least five genera of lizards known from the Morrison Formation, including *Paramacellodus*, *Dorsetisaurus*, *Schilleria*, *Saurillodon*, and *Parviraptor* (Prothero and Estes, 1980; Evans, 1996; Evans and Chure, 1999). Vertebrae of the small shartegosuchid crocodylomorph from Fruita, Colorado, are procoelous as well (Clark, in press), but the specimen from Mile 175 is smaller and less elongate and appears more likely to be that of a lizard.

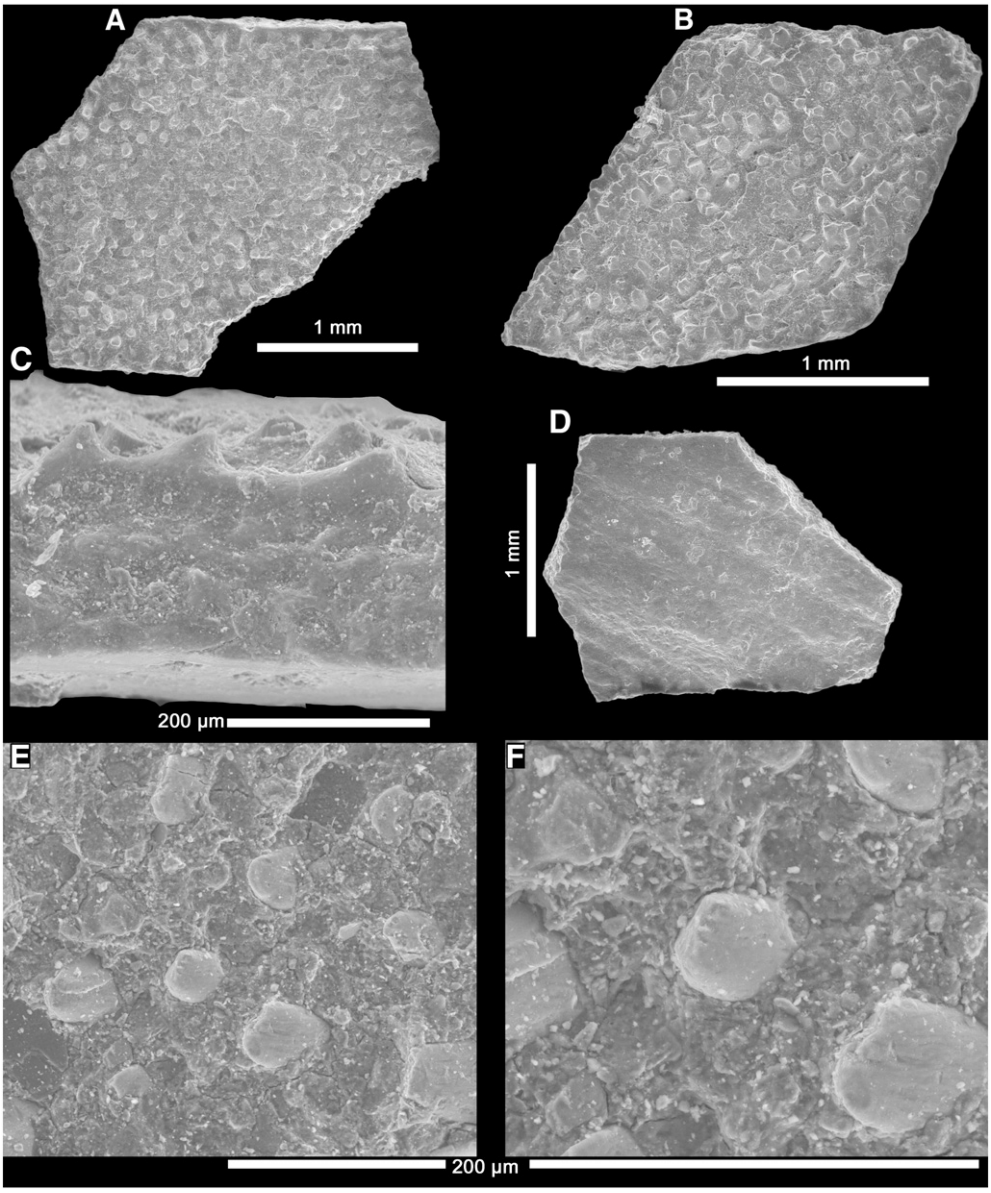

Fig. 4. Osteichthyan scales from the Morrison Formation, Mile 175 locality. A, MWC 5277A; B, MWC 5277B, both in external view. C, MWC 5277D in cross-section, D, MWC 5277C in internal view. E and F, close-ups of MWC 5277A in higher magnification views. These are similar to "second type" of Kirkland (1998) from the Fruita Paleontological Area.

5.7. Reptilia, Choristodera

Small choristoderes are represented in the sample from Mile 175 by seven vertebrae and one jaw fragment belonging to the genus *Cteniogenys* (Gilmore, 1928). The vertebrae are generally small and elongate with a deep neural canal groove divided longitudinally by a central ridge. The neurocentral sutures are almost always unfused, the neural arches missing, and the pedicels, which extend much of the length of the centrum, are mediolaterally wide near the anterior ends. One of the larger vertebrae from Mile 175 was illustrated by Foster and Trujillo (2000), who also noted that the average size of *Cteniogenys* vertebrae from the Morrison Formation appeared to be a bit larger than that from the Middle Jurassic of Kirtlington, England. The jaw fragment from Mile 175 (UW 20331; Fig. 5J–M) consists of a short section of the dorsal part of a left dentary (1.9 mm long) with two teeth attached to the dorsal surface. A third tooth was broken off at the base posterior to the intact two, and half of a shallow indentation for a fourth, anterior tooth can be seen. The bluntly conical teeth are slightly inclined posteriorly and are broken off at the tips, but they are approximately 0.55 mm in height and 0.37 mm in diameter. In lingual view (Fig. 5M) the teeth demonstrate the slightly ridged lingual surface characteristic of *Cteniogenys* (Evans, 1990; Chure and Evans, 1998).

5.8. Reptilia, Crocodyliformes

The neosuchian crocodyliforms known from the Morrison Formation include the goniopholidids *Goniopholis* and *Eutretauranosuchus* (Foster, 2003; Chure et al., 2006). Although the 67 specimens of teeth and osteoderms from Mile 175 cannot be identified to genus and are referred to Goniopholididae indeterminate, the abundance of the remains indicates a significant presence of crocodilians at the site. Again, some of the teeth are relatively small, in this case ~1–4 mm in height, but all demonstrate a typical crocodylian shape with prominent ridging on the enamel surface (Fig. 5E–I). At least some possess resorption pits and thus are interpreted as shed teeth of

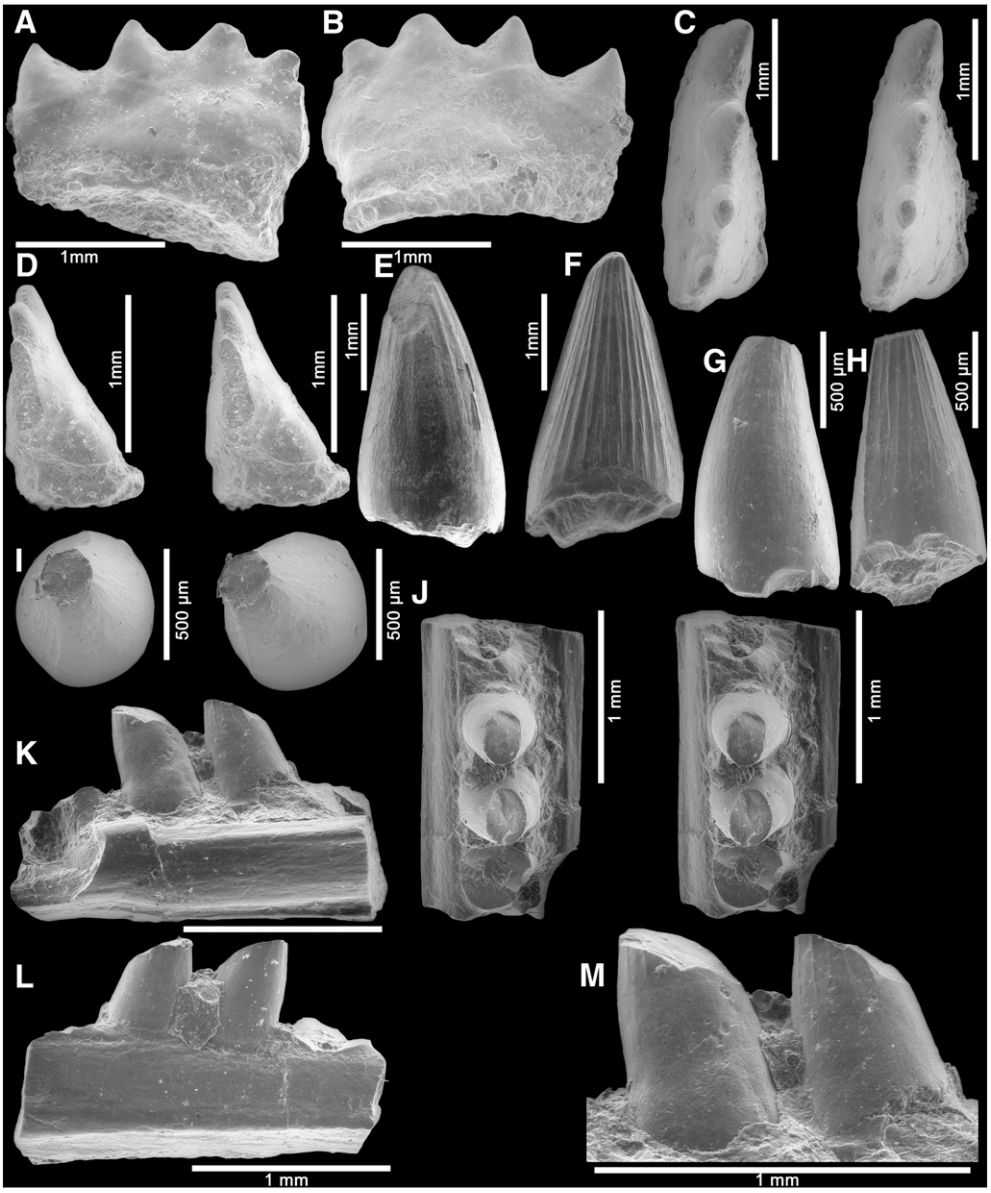

Fig. 5. Enigmatica, archosaurs, and choristoderes from the Morrison Formation, Mile 175 locality. A–D, Enigmatic tooth (Osteichthyes, Dipnoi?), possibly vomerine?, (MWC 5854) in A, concave, B, convex, C, stereo 'occlusal,' and D, stereo 'mesio-distal' views; E–F, Goniopholididae(?) indet. tooth (MWC 5951A) in E, labial, and F, lingual views; G–I, Goniopholididae(?) indet. tooth (MWC 5951B) in G, labial, H, lingual, and I, stereo occlusal views; J–M, *Cteniogenys* sp. dentary fragment (UW 20331) in J, stereo dorsal (occlusal), K, medial, and L, lateral views, with M, a close-up of teeth in labial view.

ontogenetically young animals. The small size of these fossils also indicates that relatively young animals were present.

5.9. Reptilia, Dinosauria, Theropoda

Theropod dinosaurs are represented by eight isolated teeth and tooth fragments in the Mile 175 sample. One of the more complete and small of these is UW 18237 (Fig. 6A–C), a relatively blunt-tipped, slightly recurved and laterally compressed dentary or maxillary tooth with an approximately 3.5 mm crown height. The posterior edge of the tooth is serrated from tip to root, and the anterior carina possesses serrations along its apical half. The average width of the serrations is 0.12 mm (8/mm). Based on the slightly broken wear facet on the labial side, the tooth appears to be a right dentary tooth, but this is not certain.

Although tooth shape and especially serration morphology can be very similar among distantly related theropods (Farlow et al., 1991), the overall shape of the tooth is somewhat similar to the teeth of some dromaeosaurs (Currie et al., 1990; Longrich, 2008). Such theropods may be present in the Morrison Formation based on their known occurrence in contemporaneous or even older deposits, but they have not been positively identified yet, and UW18237 certainly cannot be used to argue for their presence. But neither does the tooth appear to belong to the most abundant theropod in the formation. The recurvature of the tooth and its crown height-to-basal crown length ratio differs from those of a slightly larger, rooted tooth associated with a young juvenile *Allosaurus* skeleton from the Black Hills (Foster and Chure, 2006); UW 18237 thus probably does not represent the tooth of a juvenile *Allosaurus*, but is likely that of some other theropod. Among the other candidate theropods from the Morrison Formation *Koparion* can be ruled out due to its much different overall shape and serration morphology (Chure, 1994). That the tooth belonged to a very young individual of a larger theropod species is possible, but how teeth of tiny *Ceratosaurus* or *Torvosaurus* may have differed from those of adults is currently impossible to say, as even a young *Ceratosaurus* from Bone Cabin Quarry, collected several years ago by Western Paleo

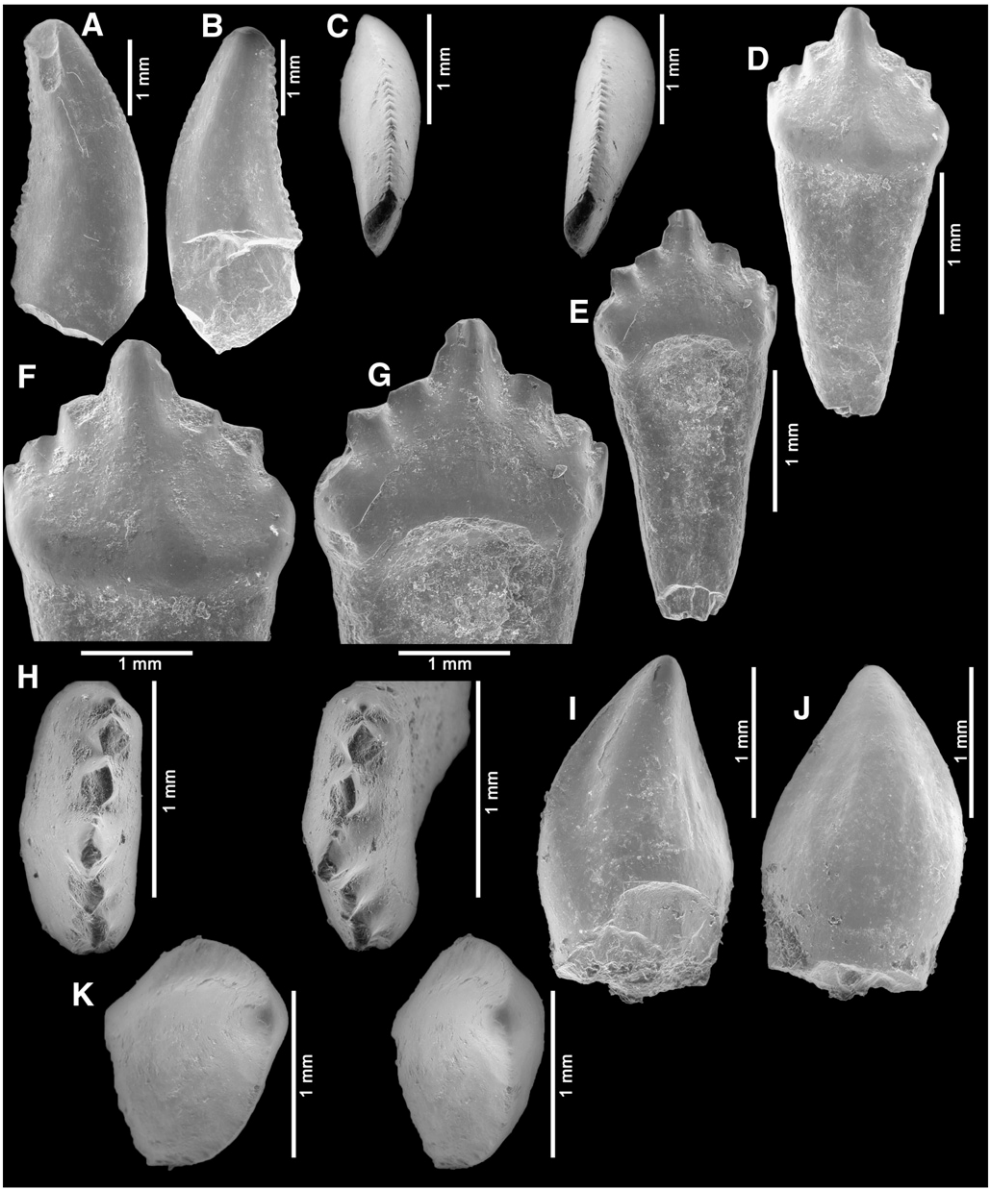

Fig. 6. Dinosaurs from the Morrison Formation, Mile 175 locality. A–C, Theropoda indet. tooth (UW 18237) in A, labial, B, lingual, and C, stereo occlusal views. D–H, *Othnielosaurus* sp. (UW 20403), D, whole tooth in labial view, E, whole tooth in lingual view, F, close-up of crown in labial view, G, close-up of crown in lingual view, H, stereo occlusal view. I–K Hypsilophodontidae indet (MWC 5851) tooth in I, labial, J, lingual, and K, stereo occlusal views.

Labs, is still much larger than this individual would have been (JRF pers. obs.). Perhaps more likely, UW 18237 belonged to one of the mid- to small-sized theropods known from the Morrison Formation such as *Coelurus*, *Orthitholestes*, *Tanycolagreus*, *Stokesosaurus*, *Marshosaurus*, or *Elaphrosaurus* (Chure et al., 2006).

5.10. Reptilia, Dinosauria, Ornithopoda

Small ornithopods are represented at the Mile 175 locality by 10 teeth. One of these, UW 20403 (Fig. 6D–H), is a small (~1 mm crown height), single-rooted bulbous maxillary or dentary tooth with an apical denticle and four (in this case broken) denticles (two on each side), a tooth form typical of hypsilophodontids (Galton, 1983, 2007). The tooth crown lacks a cingulum, and with the denticles broken off it is difficult to further identify the specimen. Among small ornithopods from the Morrison Formation, *Dryosaurus* has much different tooth shape, and *Othnielosaurus* (Galton, 2007) and *Drinker* (Bakker et al., 1990) are similar to UW 20403, but distinguishing between these two hypsilophodontids requires intact denticles. In other specimens from the sample there is no indication of the mildly tri-cusped denticles seen in *Drinker* so most of the specimens from Mile 175 probably represent *Othnielosaurus*. Dozens of teeth found by hand quarrying the Little Houston Quarry several miles to the west of Mile 175 all appear to represent *Othnielosaurus* as well (Foster, 2001), so *Drinker* may have been absent from the area during Morrison times or may be restricted to stratigraphically higher levels of the Morrison Formation.

These teeth from Mile 175 appear to be smaller, and have fewer denticles than, any other small hypsilophodontids illustrated by Galton (1983, 2007), and they probably represent some of the youngest individuals of this group yet found in the Morrison Formation.

Other phyllodont (leaf- or spade-shaped) teeth from Mile 175 include several similarly small, bulbous teeth lacking denticles (e.g., MWC 5851; Figs. 6I–K, 7). The authors interpret these as the premaxillary teeth of indeterminate hypsilophodontids.

5.11. Mammalia

Mammals are represented at Mile 175 by nine specimens, most of which are indeterminate premolars or molar fragments. However, at least one partial molar belonging to *Docodon* has been identified (UW 20578), along with a molar of an indeterminate multituberculate (probably *Ctenacodon* or *Psalodon*; UW 18027). Among the indeterminate mammalian specimens is a double-rooted premolar with a crown height just over 0.5 mm (UW 20218; Fig. 8A–D). This tooth has a single apical cusp, a distinct wear facet on the sloping posterior ridge and a lingual cingulum. It may belong to an individual in any of several groups of mammals from the Morrison Formation, such as dryolestids, paurodontids, docodonts or eutriconodonts. The small size and lack of anterior or posterior accessory cusps may indicate that it is an anterior premolar; few such teeth from mammals of the Morrison Formation have been described or illustrated, but UW 20218 is in general form most similar to paurodontids and dryolestids from the formation.

Also found in the sample were several small jaw fragments with double root sockets but no complete teeth (UW 20577, Fig. 8E–G; also MWC 5816). These jaw fragments are each approximately 3 mm long with paired alveoli for roots of three teeth (in MWC 5816 the roots are still in the alveoli but the teeth are broken off). It is thus impossible to say what types of mammals these jaws belonged to, except that the root structure would rule out dryolestids, assuming the roots are of molars and not premolars. With tooth lengths of just ~1 mm the jaws were not likely those of docodonts.

Two indeterminate teeth may represent mammalian incisors (Fig. 9). These teeth are ~1.5–2 mm in height and possess no cusps, ridges, or serrations. They are not conical, and MWC 5855 (Fig. 9D–G) is in fact somewhat spoon-shaped and reminiscent of incisors of small mammals of the Morrison Formation (Simpson, 1929). The other tooth (JRF 2000-2; Fig. 9A–C) appears to be an incisor but could conceivably be a very small canine.

There are five additional specimens that may represent mammals, including metapodial and phalanx elements, two caudal vertebrae, and a possible edentulous maxilla fragment. These are clearly not diagnostic to lower taxonomic levels.

5.12. Vertebrata indeterminate

This part of the sample includes seven small vertebrae, one small caudal vertebra, five possible eggshell fragments, all probably from indeterminate reptiles, and about 25 angular to rounded fragments of larger bones, possibly belonging to dinosaurs. Finally, there are more than 100 fragmentary vertebrate specimens that could not be identified further; these include small vertebrae, teeth, phalanges, and limb bone fragments.

6. Discussion

6.1. Paleoenvironment

Details of the paleoenvironment of Mile 175 are difficult to discern. Unlike the nearby Little Houston Quarry (Foster and Martin, 1994; Foster, 2001), the lithology of which necessitates hand quarrying and allows stratigraphic and sedimentological details to be easily viewed, the Mile 175 site is in an outcrop of very soft mudstone with few sedimentological features apparent on the surface. The fact that the site has been surface picked and had only annually-regenerated surface matrix collected for screenwashing (with only one turtle shell piece excavated in situ) means that almost no sedimentological details have been exposed by major excavation. Thus, the site's

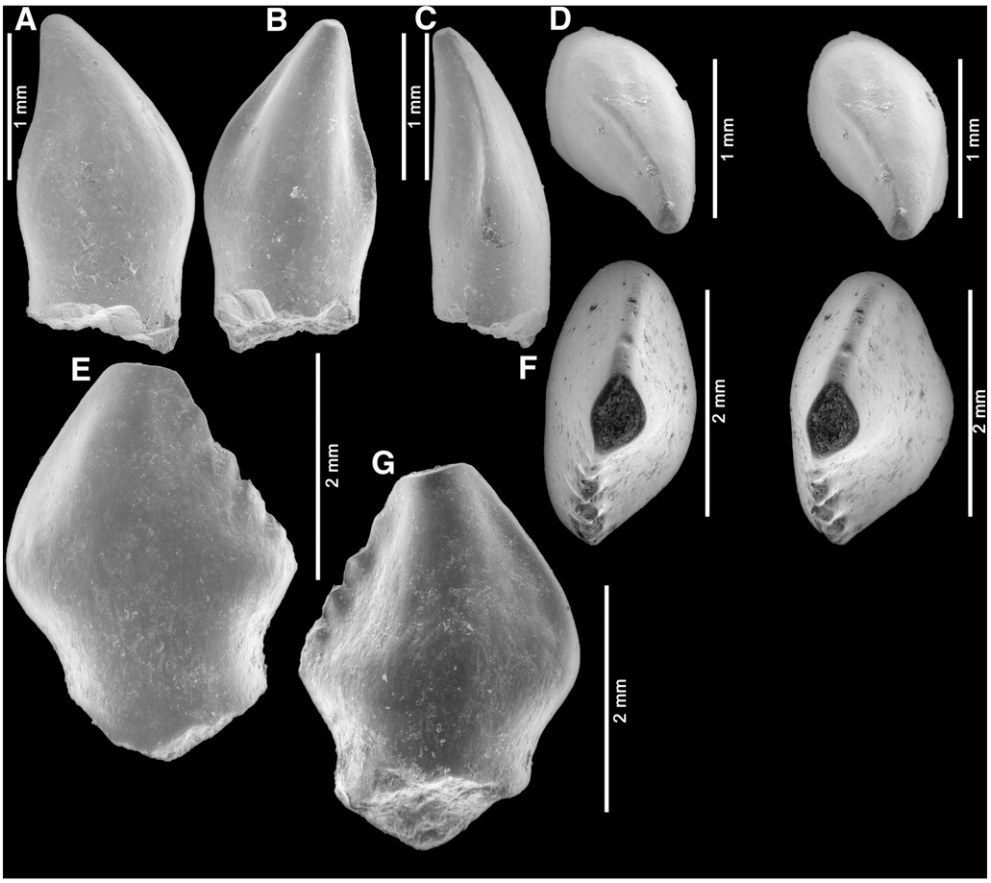

Fig. 7. Ornithischian dinosaurs from the Morrison Formation, Mile 175 locality. A–D, Hypsilophodontidae indet. tooth (MWC 5852) in A, labial, B, lingual, C, mesio-distal and D, stereo occlusal views. E–G, *Othnielosaurus* sp. tooth (MWC 5947) in E, labial, F, lingual, and G, stereo occlusal views.

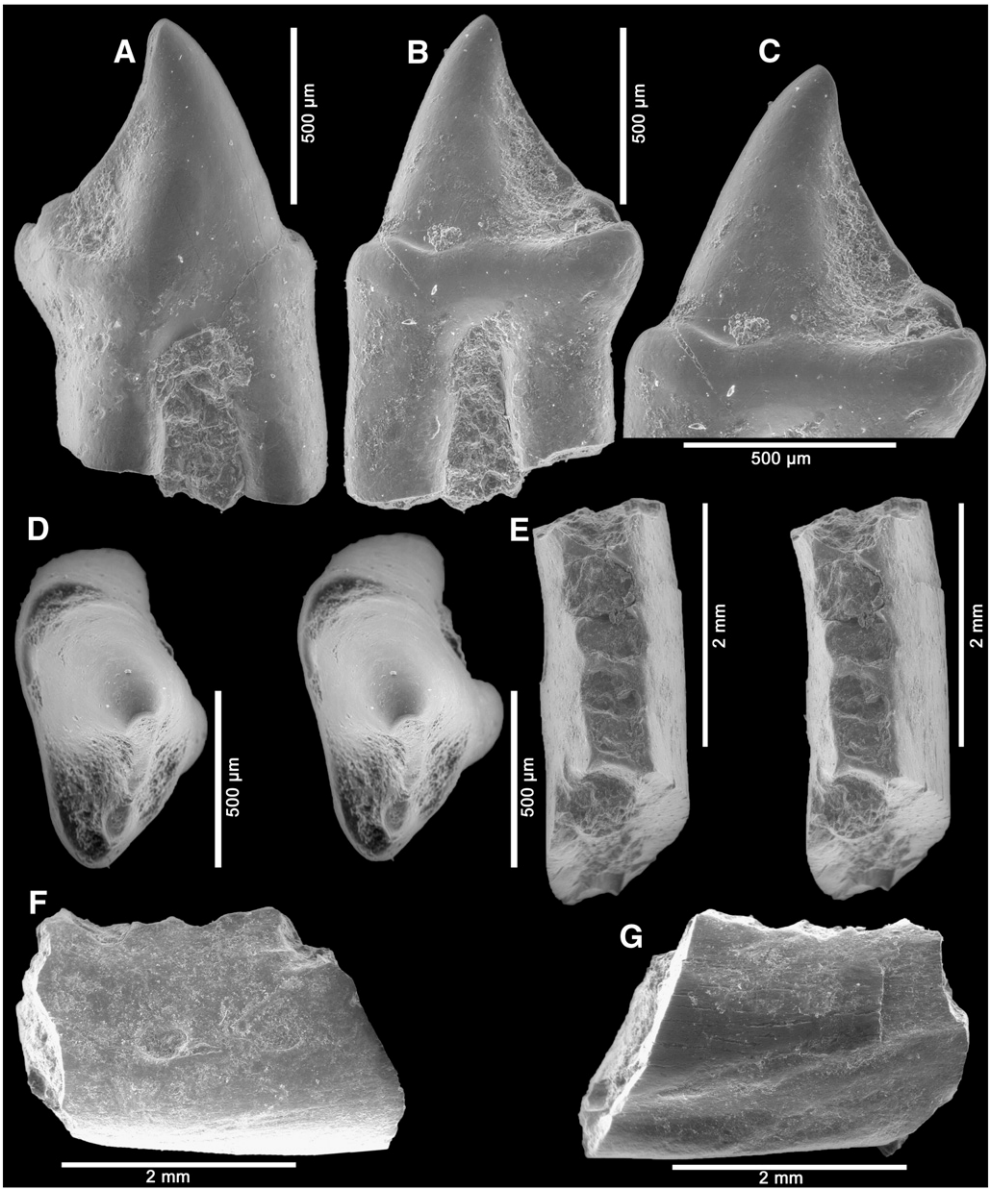

Fig. 8. Mammal fossils from the Morrison Formation, Mile 175 locality. A–D, Mammalia indet. (UW20218) premolar in A, labial, B, lingual, C, crown only in lingual, and D, occlusal views. E–G, Mammalia indet. (UW20577) jaw fragment in E, occlusal, F, lateral, and G, medial views.

paleoenvironment still has not been fully discerned. Certainly, however, the very fine-grained matrix and abundance of actinopterygian fish, turtles, and crocodilian material at the site suggest a wet setting, perhaps a perennial floodplain pond.

6.2. Diversity and preserved body size

The Mile 175 paleofauna consists of at least 14 taxa. Almost all the identifiable taxa and individuals were small. The largest taxa preserved would have been the goniopholidids or perhaps one of the theropods represented by a larger tooth fragment. Body sizes of the preserved actinopterygian fish, salamanders, lizard, choristoderes, and mammals would all have been less than 1 kg (Evans, 1990; Foster, 2003, 2009), and those of turtles probably around 5 kg at most (Dodson et al., 1980). However, even the animals with relatively larger body sizes (lungfish, turtles, goniopholidids, theropods, and ornithopods) seem to be represented at the Mile 175 site by very small and probably young individuals. A number of the *Potamoceratodus* teeth are, by both size and morphology, those of juveniles; many turtle shell fragments are of small costal pieces and demonstrate the radiating external ridges typical of juvenile individuals (Gaffney, 1979); some of the goniopholidid and theropod teeth are very small (although some of the theropod teeth may be from small adult forms); and many of the ornithopod teeth found are very small as well.

6.3. Paleobiogeography

The Mile 175 sample contains, along with the nearby Little Houston Quarry, the northernmost occurrences of both the mammal *Docodon* and the choristodere *Cteniogenys* (Foster and Trujillo, 2000; Foster et al., 2006b). It has (also along with the Little Houston Quarry) the northernmost reported occurrences of actinopterygian fish, lizards, and salamander remains in the Morrison Formation as well. The Wittecombe's Ranch locality in Wheatland County, Montana, contains the northernmost occurrence of lungfish (Foster, 2003), and the Little Houston Quarry contains the northernmost occurrence of anurans (Foster, 2001). Mammals and sphenodontians occur at the Fox Mesa site in north–central Wyoming (Brett-Surman et al., 2005),

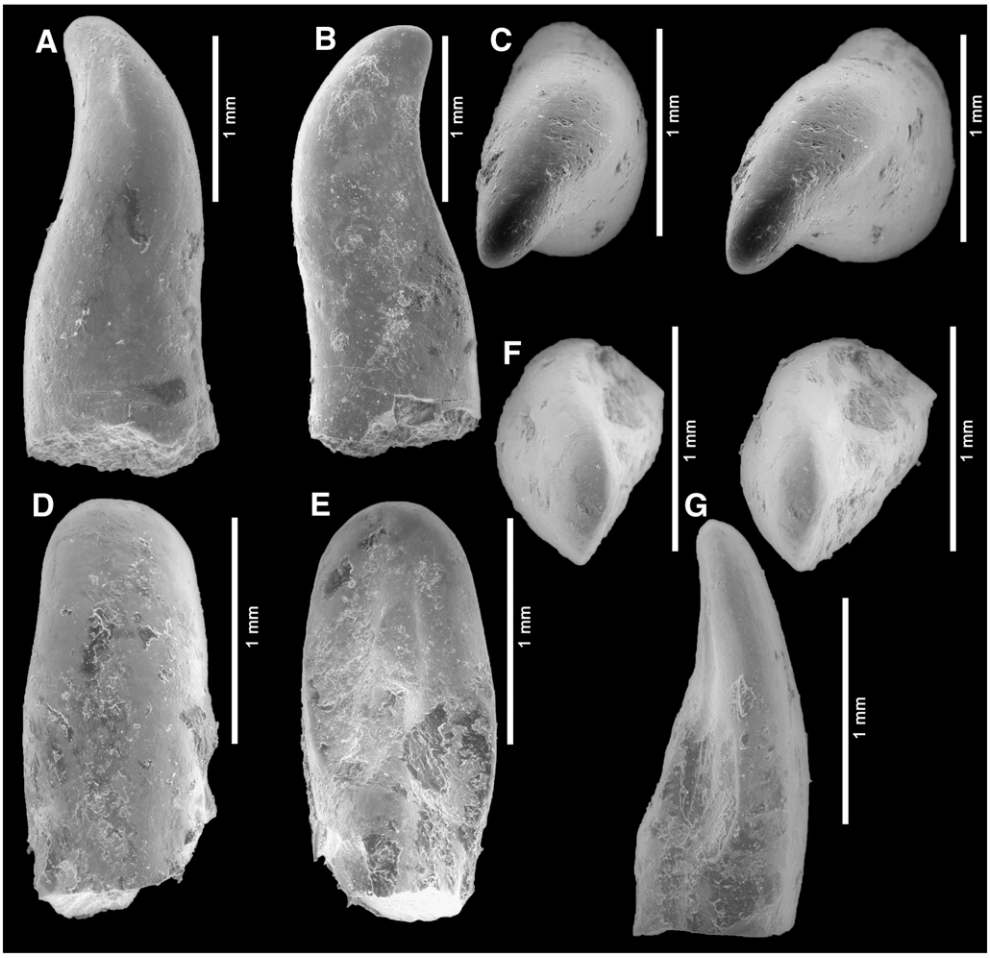

Fig. 9. Mammal(?) fossils from the Morrison Formation. A–C, Mammalia? indet. (JRF-2000-2) incisor in A, labial, B, lingual, and C, occlusal views. D–G, Mammalia indet., incisor (MWC 5855) in D, occlusal, E, lateral, F, occlusal, and G, mesio-distal views.

so this pattern is not solely an artifact of Mile 175's relatively northern location.

6.4. Fish and relative abundances

Despite a general impression that fish are rare in the Morrison Formation (perhaps resulting from the fact that indeed only the Temple Canyon, Fruita Paleontological Area, and Rabbit Valley sites have so far produced articulated material), actinopterygian fish have in fact been found at more than 20 quarries in the formation (Table 4; Kirkland, 1998; Foster, 2003). As Kirkland (1998) indicated, the widespread occurrence of actinopterygian fish fossils in the Morrison Formation and their abundance at sites like Mile 175 and Ninemile Hill argue against a lack of permanent water in this unit during the Late Jurassic. Perennial water sources must have been readily available, if not necessarily abundant, in many parts of the floodplain of the Morrison Formation. The occurrence of actinopterygian fish remains at two dozen sites in the Morrison Formation, including 42% of sites that have been screenwashed, suggests that neither these animals nor the permanent ponds and rivers they relied on for habitat were rare in the formation. Additionally, the fact that lungfish (*Potamoceratodus* spp. and *Ceratodus robustus*) occur at 10 of the sites listed in Table 4 and at nine additional sites in the Morrison Formation (Foster, 2003) and probably did not aestivate (Bakker and Bir, 2004) also suggests wet conditions in at least parts of the Morrison floodplain during the Late Jurassic. The abundance of unionid bivalves in the Morrison Formation provides additional, indirect evidence for fish, considering their reproductive (larval) reliance on fish gills for dispersal (Blazek and Gelnar, 2006; Kirkland, 2006).

6.5. Paleoecology

The sample from Mile 175 was assessed in terms of paleoecological categories (Damuth et al., 1992) of the component taxa (Table 5). The three habitat categories were: “aquatic” animals that lived full time in water (in this case including *Potamoceratodus*, although conceivably that taxon may have been able to aestivate); “semi-aquatic” tetrapods that probably spent a significant amount of their time in water; and “terrestrial” tetrapods that spent nearly all their time on land. Five feeding mode categories were used: “invertivores,” animals that were of a size and morphology that suggest they ate mostly insects, worms, grubs, or other small invertebrates, of which there appear to have been plenty in paleoenvironments of the Morrison Formation (Hasiotis, 1998; Smith et al., 2011); “invert/carnivores”, animals similar to the above category but that probably also fed on small vertebrates such as fish; “omnivores”, animals that ate both plant material and vertebrate and invertebrate meat; “carnivores”, strict consumers of vertebrate and minor amounts of invertebrate meat; and “herbivores”, animals that ate almost exclusively plants.

Analysis of the sample by these categories reveals that aquatic, semi-aquatic, and terrestrial taxa each accounted for approximately one-third of the diversity at Mile 175, but that aquatic and semi-aquatic taxa together comprised 91% of the number of identified specimens (Fig. 10). (In these analyses the 3500+ actinopterygian scales so dominated the sample that they were left out; the

Table 4
Known actinopterygian fish localities in the Morrison Formation.

Fish site	State	Fish types identified	Reference
Bone Cabin Quarry	Wyoming	Amioid	Foster (2003); MWC
East Como Bluff	Wyoming	Actinopterygii indet.	Bakker and Bir (2004)
Callison Quarry FPA	Colorado	Amioid; Actinopterygii indet.	Callison (1987)
Chuck's Prospect	Wyoming	Amioid	Prothero (1981)
Dino Nat'l Mon 11	Utah	Amioid	Foster (2003)
Dino Nat'l Mon Gen	Utah	Pycnodont; Actinopterygii indet.	Kirkland (1998)
Dry Mesa Quarry	Colorado	Actinopterygii indet.	Foster (2003)
Lindsey Quarry	Colorado	Actinopterygii indet.	Foster (2003)
Little Houston Quarry	Wyoming	Actinopterygii indet.	Foster (2001)
Locality 198 FPA	Colorado	Halecostomi	Kirkland (1998)
McKinsey-REX	Wyoming	Actinopterygii indet.	Trujillo, pers. comm.
Mile 175	Wyoming	Actinopterygii indet.	This report
Ninemile Hill	Wyoming	Actinopterygii indet.	Trujillo (1999)
Rabbit Valley	Colorado	Coccolepidae, Leptolepididae, Halecostomi	Kirkland (1998)
Rainbow Park 94	Utah	Actinopterygii indet.	Chure and Engelmann (1989)
Rainbow Park 96	Utah	Actinopterygii indet.	Chure and Engelmann (1989)
Red Fleet Reservoir	Utah	Amioid	Kirkland (1998)
Reed's Quarry 9	Wyoming	Amioid; Actinopterygii indet.	Kirkland (1998), Foster (2003), Carrano and Velez-Juarbe (2006)
Reed's Quarry 12	Wyoming	Actinopterygii indet.	Foster (2003)
Scheetz Uravan Site	Colorado	Actinopterygii indet.	Foster (2003)
Small Quarry	Colorado	Actinopterygii indet.	Foster (2003)
Stovall's Quarry 8	Oklahoma	Amioid	Kirkland (1998)
Temple Canyon	Colorado	Actinopterygii	Gorman et al. (2007)
Tom's Place FPA	Colorado	Actinopterygii indet.	Foster (2003)
Wolf Creek Quarry	Colorado	Actinopterygii indet.	Foster (2003)

actinopterygian sample consists solely of the teeth, jaw fragments, fin elements, and tooth patches.) This suggests that the area sampled by the deposit included a variety of terrestrial and aquatic habitats, but that the environment of deposition and burial of the fossils was a permanent water source. Animals that fed on a variety of resources (omnivores and invert/carnivores) account for 58% of the diversity represented at the site, strict carnivores and herbivores only 21% (Fig. 11A). However, in terms of number of identified specimens the invert/carnivores dominate (58%), with omnivores accounting for another 15% (Fig. 11B). These numbers suggest that the surrounding paleoenvironment as well as the deposit itself might have been dominated by fish and small invertebrate prey items, a conclusion also pointed to by the overall small size of the majority of the specimens and the abundance of actinopterygian fish.

The dominance of the sample from Mile 175 by aquatic and semi-aquatic animals, and the presence, but low abundance, of terrestrial vertebrates, suggest burial in a freshwater setting. The abundance of fossil material relative to the volume of host matrix studied indicates a high ratio of attritional(?) input of bone to sedimentation rate at the depositional site. Such characteristics in fine-grained settings may indicate deposition in a freshwater aquatic basin (Rogers and Brady, 2010), possibly a pond. Such conclusions are tentative, however, as the sedimentology of the Mile 175 site has only been preliminarily studied.

6.6. Screenwashing and the Morrison Formation: procedural considerations

Screenwashing operations in the Morrison Formation have historically been far less commonly pursued than major quarrying of large dinosaurs and even hand quarrying of microvertebrate sites. In part, this may be because many mudstones in the Morrison Formation are highly smectitic and such mudstones, if unweathered, can be difficult to break down during the washing process. As George Callison's crews found at the Fruita Paleontological Area, when the mudstones are broken down the vertebrate material that does survive is often of less value than the material that is hand-quarried. However, screenwashing projects may reveal elements of the faunas that are otherwise hidden. Because of their tiny size (often <1 mm), fish teeth and scales at sites such as Mile 175 and Ninemile Hill were never noticed during hand quarrying or surface picking, and thus the abundance of these materials in the samples (indeed their dominance of them) would have been missed if not for the screenwashing operations. Similarly, while pterosaur fossils are known from the Morrison Formation (Padian, 1998; King et al., 2006), the records are very sparse, and microvertebrate assemblages are likely the best way to recover these relatively small and very delicate fossils. The appearance of a tiny partial vertebra in the screenwashed sample from the Cleveland–Lloyd Quarry illustrates the potential of even traditionally dinosaur-dominated sites to produce unexpected microvertebrate taxa.

Certainly Mile 175 and Ninemile Hill screenwash more easily than many sites that have been worked for microvertebrates in the past. The mudstones at Mile 175 sites are generally non-smectitic and the bulk matrix has been taken from the surface so almost none of the rock was broken down from large, indurated blocks. Ninemile Hill, on the other hand, is very smectitic but still washes easily if sampled from the weathered top surface of the exposure (Trujillo, pers. comm., 2011). But the fact that there have so far been few sites like these worked does not necessarily mean more sites of this type cannot be found elsewhere in the Morrison Formation, at least in areas with less

Table 5
Ecological category classifications for taxa from the Mile 175 site.

Taxon	Habitat	Feeding mode
Amioid	Aquatic	Invert/carnivore
Actinopterygii A	Aquatic	Invert/carnivore
Actinopterygii B	Aquatic	Invert/carnivore
Potamoceratodus	Aquatic	Omnivore
Caudata	Semi-aquatic	Invertivore
Glyptops	Semi-aquatic	Omnivore
Dinochelys	Semi-aquatic	Omnivore
Squamata	Terrestrial	Invertivore
Cteniogenys	Semi-aquatic	Invertivore
Goniopholididae	Semi-aquatic	Carnivore
Theropoda	Terrestrial	Carnivore
Othnielosaurus	Terrestrial	Herbivore
Docodon	Terrestrial	Omnivore
Multituberculata	Terrestrial	Omnivore

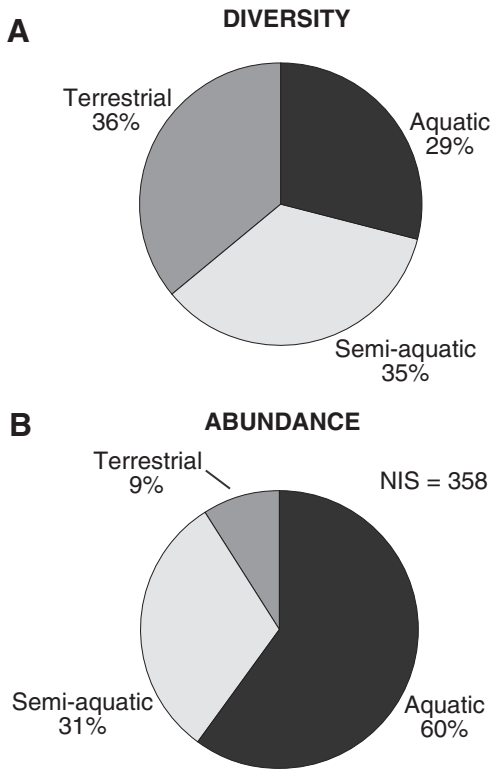

Fig. 10. Mile 175 locality, Morrison Formation. A) Taxonomic diversity of the sample by habitat preference. B) Relative abundance (number of identified specimens) of sample by habitat preference, not including fish scales.

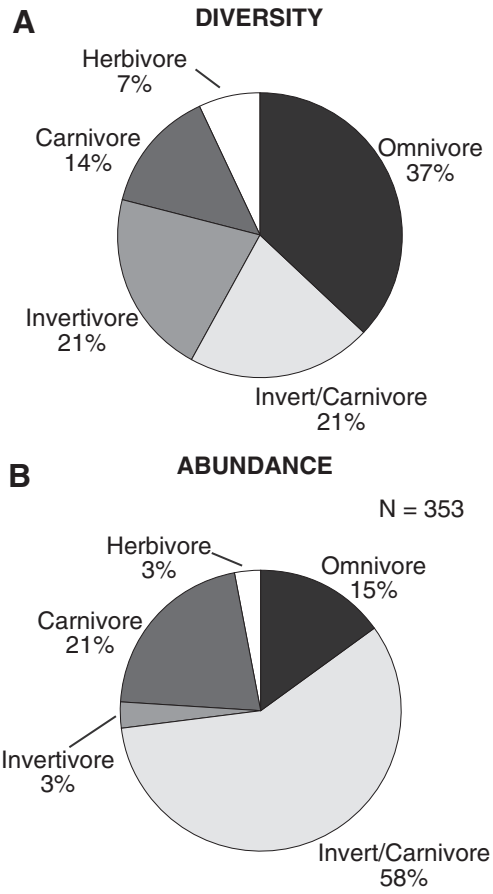

Fig. 11. Mile 175 locality, Morrison Formation. A) Taxonomic diversity of sample by feeding mode. B) Relative abundance (number of identified specimens) of sample by feeding mode.

smectitic mudstone or with weathered smectitic mudstone. These Type III microvertebrate deposits (Foster et al., 2006a) may well be widespread within the formation but their discovery will take specific searching.

Microvertebrate sites of Types I and II in the Morrison Formation consist of, respectively, thin, dense layers of disarticulated small remains in siltstones and claystones and thicker, less dense accumulations of often articulated remains in indurated claystones (Foster, 2001; Foster et al., 2006a). Type III deposits, of which Mile 175 is one, consist of fine, soft claystones that often breakdown well in water. Types I and II sites generally produce better material through hand-quarrying than through screenwashing, but the screenwashed element of the samples in each case do, the authors would argue, significantly supplement the data for the sites. For Type I deposits, screenwashing of the Quarry 9 spoil pile by Bill Turnbull revealed additional specimens there, and washing of the decade-weathered spoil pile at the Little Houston Quarry revealed a greater abundance of actinopterygian fin-ray elements than was noticeable under the microscope from the hand-quarried sample (Foster and Martin, 1994; Foster, 2001). In the case of Type II deposits, additional fish scales were located at the Fruita Paleo Area, and the Cleveland–Lloyd Quarry (which resembles Type II deposits in lithology even if it was previously lacking in microvertebrate material) yielded its first genuine microvertebrate specimen.

Problems with screenwashing mudstones in the Morrison Formation include clumping and slow breakdown of smectitic mudstones, particularly if the mudstone blocks being worked are relatively large and unweathered. Our experience, and that of the University of Wyoming and Dinosaur National Monument crews with various sites including Ninemile Hill and Rainbow Park, suggests that these challenges can eventually be overcome with repeated soaking and drying cycles of the rock, working with already naturally weathered mudstone, and, if necessary, allowing the mudstone material to weather in a controlled setting for as much as several years before washing it. The first technique worked for smectitic mudstones from the Fruita Paleo Area (8+ cycles of soaking and drying), and the last technique proved to be the key to getting the Cleveland–Lloyd Quarry mudstone to break down; when it did, the matrix yielded a reasonable number of bones for the amount of matrix that was investigated in this experimental test of the site's rock. The willingness to let the rock break down through either method requires one to accept fragmentary remains as the bulk of the ultimate sample, but this may be the only way to find identifiable microscopic material at some Morrison Formation sites, and these fossils can be just as valuable as the more complete ones at any given locality. Many screenwashing sites in the Morrison Formation may not be able to be worked in the same way that those in Upper Cretaceous rocks of North America traditionally have; for that matter, few North American Upper Cretaceous microvertebrate sites have been hand-quarried in the same way those in the Morrison Formation have. Sites in Upper Cretaceous rocks rarely yield partial skeletons or complete bones in outcrop and have largely been washed in massive campaigns of bulk washing of tons of material in order to find teeth and the rare jaws (often of mammals) that remain intact. The Morrison Formation sometimes yields complete bones or jaws and even partial skeletons of microvertebrates through hand quarrying, but can also yield even more volume of otherwise under-represented taxa through determined screenwashing.

By way of comparison, screenwashing in the Upper Triassic Chinle Group of the southwestern USA (including the Dockum Group of Texas) is the primary means of collecting small- and microvertebrates from these units (e.g., Murry, 1982, 1986; Kaye and Padian, 1994; Heckert, 2001, 2004). Chinle workers have traditionally collected large (>1000 kg) samples of bulk matrix — preparation of small

vertebrates from other quarries (e.g., Harris and Downs, 2002; Heckert et al., 2008) is the exception. Unlike the younger localities, there are few taxa as readily identifiable from isolated teeth and other elements, but Chinle microvertebrate sites are still responsible for much of the diversity of the unit. This includes the most diverse Chinle locality, the *Placerias* quarry (Kaye and Padian, 1994), Dying Grounds, Crocodile Hill, and other localities in the Petrified Forest National Park (Murry, 1989; Murry and Long, 1989; Heckert, 2004), the *Trilophosaurus* quarries and the Kalgary localities in Texas (Murry, 1982, 1986, 1989; Heckert, 2004). All of these are localities that yield faunas of larger-bodied tetrapods, but screenwashing reveals a greater diversity of small vertebrates, including an aquatic component composed of many different fish. Indeed, chondrichthyans are only known from the screenwashed faunas and osteichthyans are much more commonly recovered as isolated microvertebrates than as articulated remains (e.g. Schaeffer, 1967; Huber et al., 1993; Milner et al., 2006).

It may take patience to screenwash microvertebrate sites in the Morrison Formation, and the techniques necessary may differ from other formations, but in some cases a single bucket of matrix from the Morrison Formation may yield a surprisingly high concentration of microvertebrates. A mixture of hand quarrying with a program of screenwashing may be the best approach, as this may help bridge the taphonomic bias gap between quarrying and surface collecting (Peterson et al., 2009).

The results from this study and those of Trujillo (1999) from Ninemile Hill demonstrate that there are sites in the Morrison Formation that not only screenwash very easily but also reveal an otherwise under-represented element of the paleofauna in the abundant actinopterygian fish. The results presented here from test screenwashing of traditional hand quarrying sites such as Cleveland–Lloyd, Como Bluff, Mygatt–Moore, the Fruita Paleo Area, and the Little Houston Quarry show that such efforts may reveal important elements of the fauna even at these otherwise well known sites and that campaigns to investigate a wide range of known and as-yet unidentified sites in the Morrison Formation should significantly increase our understanding of microvertebrate sites of the Late Jurassic in general.

Acknowledgments

The Mile 175 site is on state land and is worked under a permit from the State of Wyoming's Office of Lands and Investments. Thanks to Ray Bley, Museum of Western Colorado volunteer, who dedicated about five seasons of lab work to the screenwashing and picking of many of the fossils reported here. The late Richard Peirce conducted the test screenwashing of the Mygatt–Moore Quarry matrix. Kelli Trujillo and Scott Madsen provided support and discussion in the early stages of the screenwashing operation, which was started at the University of Wyoming's paleontology facilities when the senior author was there as a postdoc; for additional support from UW we also thank Jay Lillegraven and Mike Cassiliano. Guichuan Hou of the College of Arts and Sciences microscopy facility at Appalachian State University facilitated our use of the ESEM there. Thanks also to colleagues Jim Martin and Darrin Pagnac at the South Dakota School of Mines and Technology's Museum of Geology for their help with work in the Morrison Formation of the Black Hills over the years. For discussion on other sites and specimen identifications we thank George Callison, Ken Carpenter, Dan Chure, and Toni Culver. Finally, thanks to Kelli Trujillo and two anonymous reviewers for constructive comments on the manuscript.

References

Bakker, R.T., Bir, G., 2004. Dinosaur crime scene investigations: theropod behavior at Como Bluff, Wyoming, and the evolution of birdness. In: Currie, P.J., Koppelhus, E.B., Shugar, M.A., Wright, J.L. (Eds.), Feathered Dragons. Indiana University Press, Bloomington, pp. 301–342.

Bakker, R.T., Carpenter, K., Galton, P., Siegwarth, J., Filla, J., 1990. A new latest Jurassic vertebrate fauna, from the highest levels of the Morrison Formation at Como Bluff, Wyoming. Hunteria 2 (6), 1–19.

Blazek, R., Gelnar, M., 2006. Temporal and spatial distribution of glochidial larval stages of European unionid mussels (Mollusca: Unionidae) on host fishes. Folia Parasitologica 53, 98–106.

Brett-Surman, M., Jabo, S., Kroehler, P., Carrano, M., Kvale, E., 2005. A new microvertebrate assemblage from the Upper Jurassic Morrison Formation, including mammals, theropods and sphenodontians. Journal of Vertebrate Paleontology 25 (supp 3), 39A.

Callison, G., 1987. Fruita: a place for wee fossils. In: Averett, W.R. (Ed.), Paleontology and Geology of the Dinosaur Triangle. Museum of Western Colorado, Grand Junction, pp. 91–96.

Carpenter, K., Chure, D., Kirkland, J.I. (Eds.), 1998. The Morrison Formation: an interdisciplinary study; part 2: Modern Geology, 23, pp. 1–534.

Carrano, M.T., Velez-Juarbe, J., 2006. Paleoecology of the Quary 9 vertebrate assemblage from Como Bluff, Wyoming (Morrison Formation, Late Jurassic). Palaeogeography, Palaeoclimatology, Palaeoecology 237, 147–159.

Chure, D.J., 1994. *Koparion douglassi*, a new dinosaur from the Morrison Formation (Upper Jurassic) of Dinosaur National Monument; the oldest troodontid (Theropoda: Maniraptora). Brigham Young University Geology Studies 40, 11–15.

Chure, D.J., Engelmann, G.F., 1989. The fauna of the Morrison Formation in Dinosaur National Monument. Mesozoic/Cenozoic Vertebrate Paleontology: Classic Localities, Contemporary Approaches: 28th International Geological Congress Field Trip Guidebook 1989. p. T322:8-T322:14.

Chure, D.J., Evans, S.E., 1998. A new occurrence of *Cteniogenys*, with comments on its distribution and abundance. Modern Geology 23, 49–55.

Chure, D.J., Engelmann, G.F., Madsen, S.K., 1989. Non-mammalian microvertebrates from the Morrison Formation (Upper Jurassic, Kimmeridgian) of Dinosaur National Monument, Utah–Colorado, USA. Journal of Vertebrate Paleontology 9 (supp 3), 16A–17A.

Chure, D.J., Litwin, R., Hasiotis, S., Evanoff, E., Carpenter, K., 2006. The fauna and flora of the Morrison Formation: 2006. New Mexico Museum of Natural History and Science Bulletin 36, 233–249.

Clark, J.M. in press. A new shartegosuchid crocodyliform from the Upper Jurassic Morrison Formation of western Colorado. Zoological Journal of the Linnean Society.

Currie, P.J., Rigby Jr., J.K., Sloan, R.E., 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada. In: Carpenter, K., Currie, P.J. (Eds.), Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press, Cambridge, pp. 108–125.

Damuth, J.D., Jablonski, D., Harris, J.A., Potts, R., Stucky, R.K., Sues, H.-D., Weishampel, D.B., 1992. Taxon-free Characterization of Animal Communities. In: Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.-D., Wing, S.L. (Eds.), Terrestrial ecosystems through time: Evolutionary paleoecology of terrestrial plants and animals. The University of Chicago Press, Chicago, pp. 183–203.

Dodson, P., Behrenskmeyer, A.K., Bakker, R.T., McIntosh, J.S., 1980. Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. Paleobiology 6 (2), 208–232.

Esker, D.A., 2009. An analysis of the Morrison Formation's terrestrial faunal diversity across disparate environments of deposition, including the Aaron Scott Site Dinosaur Quarry in central Utah. Unpublished master's thesis, Department of Geology, University of Cincinnati.

Evans, S.E., 1990. The skull of *Cteniogenys*, a choristodere (Reptilia: Archosauromorpha) from the Middle Jurassic of Oxfordshire. Zoological Journal of the Linnean Society 99, 205–237.

Evans, S.E., 1991. The postcranial skeleton of the choristodere *Cteniogenys* (Reptilia: Diapsida) from the Middle Jurassic of England. Geobios 24, 187–199.

Evans, S.E., 1994. A new anguimorph lizard from the Jurassic and Lower Cretaceous of England. Palaeontology 37, 33–49.

Evans, S.E., 1996. *Parviraptor* (Squamata: Anguimorpha) and other lizards from the Morrison Formation at Fruita, Colorado. In: Morales, M. (Ed.), The Continental Jurassic: Museum of Northern Arizona Bulletin, 60, pp. 243–248.

Evans, S.E., Chure, D.J., 1999. Upper Jurassic lizards from the Morrison Formation of Dinosaur National Monument, Utah. In: Gillette, D.D. (Ed.), Vertebrate Paleontology in Utah: Utah Geological Survey Miscellaneous Publication, 99-1, pp. 151–159.

Evans, S.E., Milner, A.R., Mussett, F., 1988. The earliest known salamanders (Amphibia, Caudata): a record from the Middle Jurassic of England. Geobios 21, 539–552.

Evans, S.E., Lally, C., Chure, D.C., Elder, A., Maisano, J.A., 2005. A Late Jurassic salamander (Amphibia:Caudata) from the Morrison Formation of North America. Zoological Journal of the Linnean Society 143 (4), 599–616.

Farlow, J.O., Brinkman, D.L., Abler, W.L., Currie, P.J., 1991. Size, shape, and serration density of theropod dinosaur lateral teeth. Modern Geology 16, 161–198.

Foster, J.R., 2001. Taphonomy and paleoecology of a microvertebrate assemblage from the Morrison Formation (Upper Jurassic) of the Black Hills, Crook County, Wyoming. Brigham Young University Geology Studies 46, 13–33.

Foster, J.R., 2003. Paleoecological analysis of the vertebrate fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain region, U.S.A. New Mexico Museum of Natural History & Science Bulletin 23, 1–95.

Foster, J.R., 2009. Preliminary body mass estimates for mammalian genera of the Morrison Formation (Upper Jurassic, North America). PaleoBios 28 (3), 114–122.

Foster, J.R., Chure, D.J., 2006. Hindlimb allometry in the Late Jurassic theropod dinosaur *Allosaurus*, with comments on its abundance and distribution. New Mexico Museum of Natural History and Science Bulletin 36, 119–122.

Foster, J.R., Martin, J.E., 1994. Late Jurassic dinosaur localities in the Morrison Formation of northeastern Wyoming. In: Nelson, G.E. (Ed.), The Dinosaurs of Wyoming. Wyoming Geological Association, Casper, pp. 115–126.

Foster, J.R., Trujillo, K.C., 2000. New occurrences of *Cteniogenys* (Reptilia, Choristodera) in the Late Jurassic of Wyoming and South Dakota. Brigham Young University Geology Studies 45, 11–18.
Foster, J.R., Trujillo, K.C., 2004. The small-vertebrate sample of the Morrison Formation: has collecting bias hidden a significant aquatic component in the Late Jurassic? Journal of Vertebrate Paleontology 24 (3), 59A–60A.
Foster, J.R., Carrano, M., Trujillo, K., Madsen, S., 2006a. Microvertebrate sites in the Morrison Formation (Upper Jurassic) of the western United States: definition of taphonomic modes. Journal of Vertebrate Paleontology 26 (3), 63A.
Foster, J.R., Trujillo, K.C., Madsen, S.K., Martin, J.E., 2006b. The Late Jurassic mammal *Docodon*, from the Morrison Formation of the Black Hills, Wyoming: implications for abundance and biogeography of the genus. New Mexico Museum of Natural History and Science Bulletin 36, 165–169.
Foster, J.R., Hunt, R.K., King, L.R., 2007. Taphonomy of the Mygatt–Moore Quarry, a large dinosaur bonebed in the Upper Jurassic Morrison Formation of western Colorado. Geological Society of America Abstracts with Programs 39 (6), 400.
Gaffney, E.S., 1979. The Jurassic turtles of North America. Bulletin of the American Museum of Natural History 162 (3), 91–136.
Galton, P.M., 1983. The cranial anatomy of *Dryosaurus*, a hypsilophodontid dinosaur from the Upper Jurassic of North America and east Africa, with a review of hypsilophodontids from the Upper Jurassic of North America. Geologica et Palaeontologica 17, 207–243.
Galton, P.M., 2007. Teeth of ornithischian dinosaurs (mostly Ornithopoda) from the Morrison Formation (Upper Jurassic) of the western United States. In: Carpenter, K. (Ed.), Horns and Beaks: Ceratopsian and Ornithopod Dinosaurs. Indiana University Press, Bloomington, pp. 17–47.
Gilmore, C.W., 1928. Fossil lizards of North America. Memoirs of the National Academy of Sciences, 22, pp. 1–201 (third memoir).
Gorman, M.A., Miller, I., Small, B., Pardo, J., 2007. A lacustrine Late Jurassic flora in the Morrison Formation. Geological Society of America Abstracts with Programs 39 (6), 89.
Grande, L., Bemis, W.E., 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy: an empirical search for interconnected patterns of natural history. Society of Vertebrate Paleontology Memoir: Journal of Vertebrate Paleontology, 18(supp. 1), pp. 1–690.
Harris, J.D., Downs, A., 2002. A drepanosaurid pectoral girdle from the Ghost Ranch (Whitaker) *Coelophysis* quarry (Chinle Group, Rock Point Formation, Rhaetian), New Mexico. Journal of Vertebrate Paleontology 22, 70–75.
Hasiotis, S.T., 1998. Continental trace fossils as the key to understanding Jurassic terrestrial and freshwater ecosystems. Modern Geology 22, 451–459.
Hay, O.P., 1908. The Fossil Turtles of North America. Carnegie Institution of Washington. Publication No. 75, 586 pp.
Heckert, A.B., 2001. The microvertebrate record of the Upper Triassic (Carnian) lower Chinle Group, southwestern U.S.A. and the early evolution of dinosaurs. Unpublished Ph.D. dissertation, University of New Mexico, Albuquerque.
Heckert, A.B., 2004. Late Triassic microvertebrates from the lower Chinle Group (Otischalkian–Adamanian: Carnian), southwestern U.S.A. New Mexico Museum of Natural History and Science Bulletin 27, 1–170.
Heckert, A.B., Lucas, S.G., Rinehart, L.F., Hunt, A.P., 2008. A new genus and species of sphenodontian from the Ghost Ranch *Coelophysis* quarry (Upper Triassic: Apachean), Rock Point Formation, New Mexico, USA. Palaeontology 51, 827–845.
Hembree, D.I., Hasiotis, S.T., Martin, L.D., 2005. *Torridorefugium eskridgensis* (new ichnogenus and ichnospecies): amphibian aestivation burrows from the Lower Permian Speiser Shale of Kansas. Journal of Paleontology 79, 583–593.
Huber, P., Lucas, S.G., Hunt, A.P., 1993. Late Triassic fish assemblages of the North American Western Interior. Museum of Northern Arizona Bulletin 59, 51–66.
Joyce, W.G., 2007. Phylogenetic relationships of Mesozoic turtles. Bulletin of the Peabody Museum of Natural History 48 (1), 3–102.
Kaye, F.T., Padian, K., 1994. Microvertebrates from the *Placerias* quarry: a window on Late Triassic vertebrate diversity in the American Southwest. In: Fraser, N.C., Sues, H.-D. (Eds.), In the Shadow of Dinosaurs: Early Mesozoic Tetrapods. Cambridge University Press, Cambridge, pp. 171–196.
Kielan-Jawarowska, Z., Cifelli, R.L., Luo, Z.-X., 2004. Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure. Columbia University Press, New York.
King, L.R., Foster, J.R., Scheetz, R.D., 2006. New pterosaur specimens from the Morrison Formation and a summary of the Late Jurassic pterosaur record of the Rocky Mountain region. New Mexico Museum of Natural History and Science Bulletin 36, 109–113.
Kirkland, J.I., 1987. Upper Jurassic and Cretaceous lungfish tooth plates from the Western Interior, the last dipnoan faunas of North America. Hunteria 2 (2), 1–16.
Kirkland, J.I., 1998. Morrison fishes. Modern Geology 22, 503–533.
Kirkland, J.I., 2006. Fruita Paleontologica Area (Upper Jurassic, Morrison Formation), western Colorado: an example of terrestrial taphofacies. New Mexico Museum of Natural History and Science Bulletin 36, 67–95.
Longrich, N., 2008. Small theropod teeth from the Lance Formation of Wyoming, USA. In: Sankey, J.T., Baszio, S. (Eds.), Vertebrate Microfossil Assemblages: Their Role in Paleoecology and Paleobiogeography. Indiana University Press, Bloomington, pp. 135–158.
Mapel, W.J., Gott, G.B., 1959. Diagrammatic restored section of the Inyan Kara Group, Morrison Formation, and Unkpapa Sandstone on the western side of the Black Hills, Wyoming and South Dakota. United States Geological Survey Mineral Investigations, Field Studies Map MF-218.
Mapel, W.J., Pillmore, C.L., 1963. Geology of the Inyan Kara Mountain quadrangle, Crook and Weston Counties, Wyoming. United States Geological Survey Bulletin 1121, M1–M56.
Marsh, O.C., 1878. New species of *Ceratodus* from the Jurassic. The Annals and Magazine of Natural History 1 (5), 184.
Milner, A.R.C., Kirkland, J.I., Birthisel, T.A., 2006. The geographic distribution and biostratigraphy of Late Triassic–Early Jurassic freshwater fish faunas of the southwestern United States. New Mexico Museum of Natural History and Science Bulletin 37, 522–529.
Murry, P.A., 1982. Biostratigraphy and Paleoecology of the Dockum Group, Triassic of Texas. Southern Methodist University, Dallas. 459 pp.
Murry, P.A., 1986. Vertebrate paleontology of the Dockum Group, western Texas and eastern New Mexico. In: Padian, K. (Ed.), The Beginning of the Age of Dinosaurs: Faunal Change across the Triassic–Jurassic Boundary. Cambridge University Press, Cambridge, pp. 109–137.
Murry, P.A., 1989. Paleoecology and vertebrate faunal relationships of the Upper Triassic Dockum and Chinle Formations, southwestern United States. In: Lucas, S.G., Hunt, A.P. (Eds.), Dawn of the Age of Dinosaurs in the American Southwest. New Mexico Museum of Natural History, Albuquerque, pp. 375–400.
Murry, P.A., Long, R.A., 1989. Geology and paleontology of the Chinle Formation, Petrified Forest National Park and vicinity, Arizona and a discussion of vertebrate fossils of the southwestern Upper Triassic. In: Lucas, S.G., Hunt, S.G. (Eds.), Dawn of the Age of Dinosaurs in the American Southwest. New Mexico Museum of Natural History, Albuquerque, pp. 29–64.
Padian, K., 1998. Pterosaurians and ?avians from the Morrison Formation (Upper Jurassic, western U.S.). Modern Geology 23, 57–68.
Pardo, J.D., Huttenlocker, A.K., Small, B.J., Gorman, M.A., 2010. The cranial morphology of a new genus of lungfish (Osteichthyes: Dipnoi) from the Upper Jurassic Morrison Formation of North America. Journal of Vertebrate Paleontology 30, 1352–1359.
Patterson, C., 1982. Morphology and interrelationships of primitive actinopterygian fishes. American Zoologist 22, 241–259.
Peterson, J.E., Scherer, R.P., Huffman, K.M., 2009. Methods of microvertebrate sampling and their influence on paleoecological interpretations: preliminary results of a standardized experiment. Geological Society of America Abstracts with Programs 41 (7), 628.
Prothero, D.R., 1981. New Jurassic mammals from Como Bluff, Wyoming, and the interrelationships of non-tribosphenic Theria. Bulletin of the American Museum of Natural History 167 (5), 281–325.
Prothero, D.R., Estes, R., 1980. Late Jurassic lizards from Como Bluff, Wyoming and their palaeobiogeographic significance. Nature 286, 484–486.
Rogers, R.R., Brady, M.E., 2010. Origins of microfossil bonebeds: insights from the Upper Cretaceous Judith River Formation of north–central Montana. Paleobiology 36, 80–112.
Russell, D.A., 1989. The Dinosaurs of North America. NorthWord Press, Inc., Minocqua. 240 pp.
Schaeffer, B., 1967. Late Triassic fishes from the western United States. Bulletin of the American Museum of Natural History 135, 287–342.
Schaeffer, B., Patterson, C., 1984. Jurassic fishes from the western United States, with comments on Jurassic fish distribution. American Museum Novitates 2796, 1–86.
Schultze, H.-P., 1996. The scales of Mesozoic actinopterygians. In: Arratia, G., Viohl, G. (Eds.), Mesozoic Fishes: Systematics and Paleoecology. Verlag Dr. Friedrich Pfeil, Munich, pp. 83–93.
Simpson, G.G., 1929. American Mesozoic Mammalia. Memoirs of the Peabody Museum of Yale University 3, 1–235.
Small, B.J., Gorman, M.A., Pardo, J., Smith, D., 2007. A Late Jurassic lacustrine biota from the Morrison Formation of Colorado. Geological Society of America Abstracts with Programs 39 (6), 400.
Smith, A.S., Zatoń, M., 2007. The first Actinopterygian (Pisces: Osteichthyes) tooth from the Bathonian (Middle Jurassic) of the Polish Jura (south–central Poland). Freiberger Forschungshefte 15, 35–40.
Smith, D.M., Gorman, M.A., Pardo, J.D., Small, B.J., 2011. First fossil Orthoptera from the Jurassic of North America. Journal of Paleontology 85, 102–105.
Steel, R., 1973. Crocodylia. Handbuch der Paläoherpetologie, part 16. Gustav Fischer Verlag, Stuttgart. 116 pp.
Trujillo, K.C., 1999. Vertebrate paleontology, stratigraphy, and sedimentology of new microvertebrate localities in the Morrison (Upper Jurassic) and Cloverly (Lower Cretaceous) formations, Ninemile Hill, Carbon County, Wyoming. Unpublished master's thesis, Department of Geology and Geophysics, University of Wyoming, 90 p.
Tway, L.E., 1984. A coded system for identifying Paleozoic ichthyoliths. Journal of Vertebrate Paleontology 3 (4), 187–199.
Tway, L.E., Harrison, W.E., Zidek, J., 1986. Thermal alteration of microscopic fish remains — an initial study. Palaios 1, 75–79.
Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), 2004. The Dinosauria, Second Edition. University of California Press, Berkeley.